

ANNUAL CYCLE OF THE BLACK-CAPPED CHICKADEE—3

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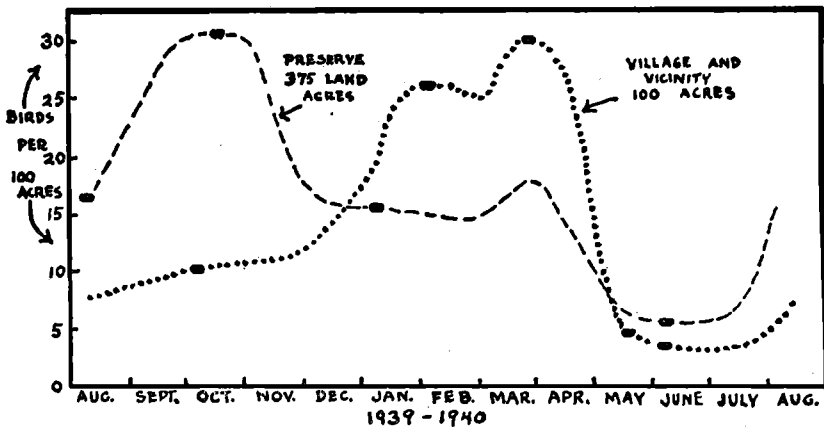
THE two previous parts of this paper (Auk, 58: 314–333 and 518–535) were concerned with the activities of Black-capped Chickadees (*Penthestes atricapillus atricapillus*) on the Huyck Preserve and vicinity during the breeding season, which, in one phase or another, covered nearly half the year from March to August. The present and concluding part deals with the non-breeding half of the year, in which a study of flocking and general behavior received special attention. Much time was spent throughout the autumn and winter in following the flocks in the field, charting their movements on mimeographed maps, making censuses, and recording everything that could be observed. During the winter, trapping and color banding were carried on at four stations, two in the village and one at each end of the elongated Preserve (see Text-figure 3). No feeding stations were operated in the central part of the Preserve, an area left as a 'control' without artificial feeding (nor were stations operated here in previous years). One of the winter village flocks was singled out for special day by day observation and for experimental work.

POPULATION TRENDS

In analyzing autumn and winter behavior it is important to consider the seasonal changes in population which are summarized in Text-figure 2. The data on total populations previously given are here reduced to a common figure of birds per 100 acres (or 40 hectares). Also, these data refer to density in the total land area including all habitats (see Text-figure 3); at certain seasons chickadees frequented all parts of the study area, while in summer they were more restricted in regard to habitat. Each rectangular point on the graph represents the population density at a specific time of year as determined by a series of censuses of the entire areas and by banding. The broken lines connecting the points are the partly hypothetical trends which were believed to have occurred as evidenced by movement of banded birds and by censuses over parts of the areas. The curve as a whole, therefore, pictures in a diagrammatic way the major seasonal changes in population which occurred during the year. Population was most stable during mid-winter and early summer when the great majority of individuals remained within restricted areas; hence, population could be more

accurately determined during these fixation periods. At other seasons, particularly late summer and autumn, the population was not only larger but many individuals were not fixed in their movements; hence, population was more variable and more difficult to determine on a comparative basis.

The important points to note from Text-figure 2 are: (1) Population on the Preserve (essentially a natural upland wooded area) was greatest during late summer and autumn while a peak was reached in the village (an area of shade trees, shrubbery and feeding



TEXT-FIGURE 2.—Seasonal variation in the Chickadee population of the Preserve as compared with the village vicinity. See text for explanation.

stations located in the valley) during the winter. (2) In both areas the population was greater in winter than in summer, but the difference was more marked in the village, the winter-summer ratio being approximately 2.5 to 1 on the Preserve as compared with 8 or 10 to 1 in the village vicinity. These relations suggest that there may be a well-marked seasonal movement from forested hills and swamps to settled valleys and other places of winter concentration; this was also indicated by the dispersal of birds from the village to the surrounding country which was actually observed in the spring. Much has been written concerning the migratory status of the chickadee in the Northeast and the various lines of evidence have been recently summarized by Wallace (1941). Most of the evidence, including banding results in the present study, boils down to the following: (1) Adults tend to remain fixed during both

¹ Text-figure 1 appeared with Part 1 of this paper in *The Auk*, 58: 316, July, 1941.

winter and summer but may (or may not) move at least locally during the spring and autumn; (2) Immature birds of the year range widely and apparently irregularly during late summer, autumn, and perhaps to a lesser extent during winter and spring, rarely remaining in or returning to the area of their birth. Therefore, a given chickadee flock may contain a relatively stable element,—the local adults,—and/or a relatively unstable element, the first-year birds. These relations, together with the expected population increase following the breeding season, seem adequate to account for a population curve such as shown in Text-figure 2 and to clarify certain aspects of flock behavior.

For comparison, a few estimates of the abundance of chickadees in other localities are listed below, although few attempts have been made to determine the year-round picture.

Reference	Area	Locality	Birds per 100 acres	
			winter	summer
Butts (1931)	1 sq. mile semi-wood- ed country	Ithaca, N. Y.	20	4.7
Butts (1931)	80-acre Fuertes Sanctuary	Ithaca, N. Y.	38	5
Williams (1936)	65 acres climax beech-maple	Cleveland, Ohio	24.6	12.3
Forbes and Gross (1923)	58 acres open woodlands	Northern Ill.	10.3
Bird (1930)	Aspen forest	Manitoba	6.2
Van Deventer (1936)	Mendon Pond Park	Western N. Y.	19.5
Saunders (1936)	Beech-maple, oak- hickory, cherry- aspen forests	Allegheny State Park, N. Y.	9.4

Wallace (1941) reported the lowest winter population in three years of study at Lenox, Massachusetts, during the winter of 1939–40, but does not give figures in terms of population per unit area.

VOICE

Vocal activity is extremely important in regulating the behavior of chickadees, especially during the flocking season. Like the Corvidae, chickadees have a large vocabulary. Many, if not most, of the notes seem to have definite functions, that is, they are given under particular conditions and frequently produce definitely observable responses. The following are those which the writer has been able to distinguish clearly. The list does not by any means cover all the utterances made by the species. Variations and intermediate

notes are sometimes heard which on further study may prove to have special functions. Some of these notes have been mentioned previously in this paper but all are listed here for completeness.

1. *The phoebe song*.—A high-pitched clear whistle of two or three notes, *phoe-be* or *phoe-be-be*, uttered by both sexes but more frequently and louder by the male. The *phoebe* song was heard sparingly throughout the year but most often in the spring during pre-nesting activities. As previously discussed, loud songs given by males function in courtship and in territory defence. In late summer and early autumn a hoarse, sometimes imperfect whistle is given extensively by juveniles. During the autumn and winter the song was rarely heard, although on several occasions whistles were given just before birds went to roost. I have noted that the same individual may change the pitch of the whistle or change from two to three notes as Saunders (1935) has described.

2. *The signal song*.—Exactly like the regular song but much softer and sometimes reduced to one note. This much subdued song is given by the male (rarely by the female) when approaching the nest. Either sex may give soft whistles under conditions of excitement as, for example, when the young are leaving the nest.

3. *General call note*.—The familiar *chick-a-dee-dee-dee* is uttered by both sexes throughout the year, but most frequently during the flocking period. Use of this note seems to announce the whereabouts of the bird to others. When one bird becomes lost from the flock, or the flock becomes scattered, this note is frequently given with the result that the flock tends to consolidate again. The same was observed when members of a breeding pair became separated in feeding excursions. There are a number of variations of the chickadee call, some of which have special meanings as listed below.

4. *The scolding note*.—A loud, rapidly given *chick-a-dee-dee-dee-dee* with emphasis on the *dee* part. The scolding note is similar to the general call note but easily distinguishable by the more emphatic tone and lower pitch. This note is heard when the nest is attacked or an enemy such as a cat or an owl is sighted. Other chickadees or species respond by coming up to scold or attack the enemy.

5. *The fighting note*.—A sputtery, high-pitched, beady *chick-a-dee* or *chit-chit-chit* (repeated a varying number of times). This note was frequently heard during spring 'fights' between pairs and during the chasing and fighting phases of territory defence. The note seems to indicate a higher degree of emotional stress and anger than no. 4.

6. *The alarm note*.—An explosive, short *chick-a-dee* or *chit-chit*.

This note is given when an enemy appears at close quarters or attacks suddenly, especially if the bird is feeding on the ground or in the open. The alarm note is usually accompanied by a dash for cover; other birds following the example. Thus, this note, although similar to the above, produces the opposite reaction and seems to express fear rather than anger.

7. *The recognition or contact note.*—A thin, weak *tseep* or *tseet* is the most frequently uttered note in the vocabulary, heard at all times of the year from both sexes. The contact note is uttered more or less continually and seemingly automatically by birds in the flock and by mated pairs, especially during feeding excursions. Single birds may also give the note, but presence of companions results in increased frequency. It was noted that the frequency of *tseep* calling decreased in very cold weather, when birds were resting or preening, and when engaged in feeding the young. The *tseep* call seems to serve to keep birds in close communication with each other.

8. *The flight or restless note.*—A thin, weak *tsleep* or *tsleet* somewhat higher-pitched and louder than the contact note, and usually easily distinguished from it. This note is uttered just before extended movements or flights across open spaces. Usually one can safely predict that the flock or individual is going to move from one place to another when this note is heard. In the flock, after one bird calls repeatedly, others often follow suit and the flock moves as a whole.

9. *The warning note.*—A thin, very high-pitched *tsee* repeated several times. This note may follow the alarm note when a hawk attacks, or more frequently it is given without the alarm note when a hawk appears or any large bird flies over or casts a shadow. Chickadees and also other species (warblers, kinglets, etc.) respond to this note by 'freezing,' that is, remaining perfectly motionless. In the case of a hawk or shrike attacking, the birds may remain 'frozen' for as long as ten minutes and can almost be touched before they will move. When the bird causing the warning is a crow or a woodpecker, chickadees 'freeze' momentarily or not at all. The 'freeze' is usually broken when one bird calls *chick-a-dee*; almost immediately the flock becomes active again. I have never heard the warning call given at the approach of an enemy on the ground; it is apparently specialized for winged enemies.

10. *The dominance note.*—A throaty *che-lùp* or *che-ùp-che* which may be given by either sex but most often by aggressive males. This note is apparently a 'vocal threat' used when birds come close together or when one bird chases another. It is frequently heard at feeding

stations when two or more birds attempt to feed at the same time; a dominant bird may put to flight a subordinate bird simply by using this note. The dominance note is also given under natural conditions when one bird displaces another, and along with other notes during courtship and territory quarrels.

A number of gurgling, semi-musical notes have been heard which are apparently variations of the dominance note. These were given particularly in the spring and by juveniles in late summer without being directed at another bird or producing an observable response. If anything, they apparently express a condition of general vigor.

11. *A musical to-will.*—This call was frequently heard during the spring and during the flocking period, often in connection with calls nos. 3 and 10. However, its function was not evident.

12. *The begging note.*—A loud *tee-shìp* or *tee-shìp-she*, given by young from the time they leave the nest until independent of the parents, and by the female during egg laying and incubation (more rarely at other times during breeding season). Begging by both young and the female is often accompanied by a fluttering of the wings.

13. *The mating (?) note.*—A high-pitched, rolling twitter accompanied by fluttering of wings. This note uttered by the female was heard just before and during copulation and also during ceremonies preceding pairing in one case. This note with wing-fluttering accompaniment was also frequently given by both sexes when the pair met close to the nest.

14. *The 'perplexed' note.*—A very low guttural sound given by the adults when some strange object or person was near the nest. When birds gave this note they appeared to be puzzled rather than alarmed.

15. *The 'hissing' or 'bluff' note.*—Rather the result of a forced expiration than a vocal effort. Incubating females and nestlings between the ages of 12 and 17 days sometimes puff up and 'hiss' at the intruder when the nest is approached closely, as Thoreau has described.

16. *The distress call.*—A loud squeal similar to the distress call of a baby chick. I have heard this only from nestlings which had been captured after leaving the nest. The call released notes nos. 4 and 5 together with injury-feigning behavior on the part of the parents.

Many of the above chickadee notes do not seem to be generally recorded in the literature. Thus, Forbush (1929) lists only four notes (nos. 1, 3, 10 and a rare "singing like a ruby-crowned kinglet" which I have not heard), and Saunders (1935) likewise lists four (nos. 1, 3, 7 and 10). However, comparable notes have been described for other species. Davis (1940) lists thirteen notes for the

Smooth-billed Ani (*Crotophaga ani*), a markedly social species, some of which are comparable in function to chickadee notes. The Ani, for example, has a different note (*and different accompanying behavior*) for a hawk and an enemy on the ground. Erickson (1938) lists a dozen or so notes for the Wren-tit (*Chamaea fasciata*), most of which have corollaries with the chickadee notes. Hann (1937), on the other hand, lists but four or five call notes (other than songs) for the Oven-bird (*Seiurus aurocapillus*), generally a non-social species.

Many of the chickadee's notes, although sometimes having very different functions, have apparently developed from a given type of vocal utterance. Thus, notes nos. 1 and 2 are *phoebe* notes; nos. 3, 4, 5, and 6 are variations of the *chick-a-dee* call; nos. 7, 8, and 9 are *tseet* notes. Also, the same note may have different functions at different seasons (no. 1 and probably 10). Consequently, variations of a few basic notes give the chickadee a considerable means of vocal communication. Of the sixteen notes listed, about eight are concerned primarily with breeding behavior and eight function primarily in general social relations.

The part that these notes play as 'signals' (Tinbergen, 1939) or 'releasers' (Lorenz, 1935, 1937) is evident from the above descriptions. Lorenz (1937) lists six releasing functions of the social companion; it is interesting to note that the chickadee has a call note which functions in five if not all six of these as follows: (1) inducing 'contagion' or 'imitation,'—perhaps call note no. 8; (2) the release of following reactions,—notes no. 3 and 8; (3) response to warning,—no. 6 and 9; (4) social attack reactions,—no. 4; (5) pecking-order reactions,—no. 10; (6) response to disappearance of a companion,—no. 3. Thus, chickadees, perhaps more than larger or more conspicuously plumaged birds, depend on stimuli in the acoustical rather than the optical field in synchronizing the activities of the flock members.

FLOCK BEHAVIOR

Chickadee flocks are rather loose aggregations of individuals; occasionally the flock is fairly compact and moves with a fair degree of precision, but usually it is a straggling affair. When a flock crosses an opening, for example, birds pass over singly or in twos or threes and it may require ten minutes before a flock of a dozen birds passes from one side to the other. Abundant observation has convinced me that the chickadee is a strong individualist but at the same time has considerable social tendencies during non-breeding periods; consequently, its flocking tendencies are intermediate between

those of strictly non-social species and of such a highly social species as the European Jackdaw in which the flock is well organized and behaves as a 'super-individual' (Lorenz, 1935).

Size and individual composition of the flock.—The number of birds in a flock is often difficult to determine, especially in thick woods. However, by keeping slightly ahead of the flock as it moved it was frequently possible to obtain accurate counts of the birds as they passed across openings in the forest, crossed roads, or moved along hedgerows. Such counts of flocks in the woods together with counts of banded birds at village feeding stations may be summarized as follows:

	<i>Number of observations</i>	<i>Average birds per flock</i>	<i>Variation</i>
Autumn (Sept. and Oct.)			
Natural flocks on Preserve	33	8	2-20
Winter (Jan. and Feb.)			
Natural flocks on Preserve	16	7	2-16
Village feeding stations	20	12	8-16

Single birds seen every now and then in both autumn and winter are not included in the above averages. Two things of interest seem to be indicated by these data. First, although the population was largest on the Preserve during the autumn, flocks averaged only slightly larger (however, the largest flocks were recorded during this season, these being counterbalanced by small flocks also frequently encountered). In other words, the larger autumnal population resulted partly in larger flocks but mostly in more numerous flocks as was also observed in census work. For example, a rapid cruise of the Preserve on October 19 revealed seventeen flocks, while on January 10 but seven flocks could be located. Secondly, the flocks around feeding stations in the village were larger than those occurring under natural feeding conditions.

Wallace (1941) reports that the 'standard' chickadee flock at Lenox, Massachusetts, is six to eight individuals in winter, which is approximately the same size of flocks reported by W. P. Smith in Vermont and by Whittle in Massachusetts (see Wallace, 1941). Butts (1931) considered the number in a complete flock to be about fifteen on his study area at Ithaca, New York. He did not believe the abundant feeding stations present had any effect on the number of birds although he had no control area (without feeding stations) to test this assump-

tion. Both Wallace (1941) and Mrs. F. N. Hammerstrom (1942), on the other hand, report that good stations operated over several years may build up a large patronage. As Wing (1941) has pointed out, groups of birds held together by a common attraction of the environment (concentrated food supply or limited habitat, for instance) should probably be considered 'congregations' rather than true flocks in which birds associate because of a gregarious urge.

While seven or eight is apparently the average-sized natural flock at this latitude this average has more of a theoretical than actual significance for two reasons: (1) flocks of four to five or ten to fifteen are as frequently encountered as groups of seven or eight. (2) A flock is not permanently fixed in size, but may vary from day to day or even from hour to hour. Even in winter when most individuals remain within remarkably limited ranges flocks break up and re-form or individuals pass from one flock to a neighboring one as is readily observed when flocks are followed for long periods of time. Frequently, individuals or several individuals were observed to lag behind or become detached from the flock. Usually, much calling back and forth resulted as if the birds were torn between the desire to follow the flock or to have the other birds follow them! Sometimes one or the other of the detachments would 'win out' and the flock would consolidate; at other times the two portions would remain separate, perhaps to join later. The following observation condensed from field notes indicates how contact by separate flocks may influence composition of the flock:

February 1, 7:05 to 9:30 a. m.—Follow chickadee flock in Lincoln Pond woods from time of leaving roost. Accurate count at 9:28 shows eleven chickadees present. 9:57.—Another flock comes from northern part of woods and two groups join after much calling and milling around. 12:00.—Large flock still intact, birds feeding in hemlock trees; count shows 27 chickadees present. 12:55.—Flock splits, one group moves rapidly north, the other south. Accurate count shows fourteen birds in south group, apparently three birds from north group have joined the south flock at least temporarily.

The study of banded birds in winter showed that some individuals had a greater tendency to become detached from the flock or to pass from one area to another than did other individuals. In the autumn with numerous unsettled juveniles, this variation is probably even more marked.

Chickadee flocks do not seem to have definite leaders, which may have some bearing on the partial instability of the flocks. Birds seem to follow first one individual then another. Probably they tend to follow the individual which acts or calls most forcibly, or

as Lorenz (1935) comments, that individual which 'knows what he is about.'

To sum up, factors which result in partial instability of the flock are: lack of definite organization or leadership within the flock, individualistic tendencies of the birds (see subsequent discussion of dominance), and tendency of some individuals to wander especially in late summer and autumn. On the other hand, factors which tend to keep the flock intact are: social or gregarious tendencies of the species, strong development of vocal signals, and strong tendency of many individuals to remain in a restricted area. Apparently, a counterbalance of these tendencies results in the usual small-sized flock. Thus, the larger the flock, the more apt it is to split up; likewise, the smaller the flock the more apt it is to join with other birds provided there are others in or near the cruising range. Where chickadees are scarce the flocks will, of course, be small. As already pointed out, large groups of birds around feeding stations may be congregations rather than true flocks. Very large flocks, however, have been reported during migration or emigration of birds in the northern part of the range (see Butts, 1931).

It should be pointed out that territorial behavior, that is, defence behavior on the part of individuals of the flock, does not seem to play any part in determining the size of the flock. Although social-dominance reactions occur, birds during the non-breeding season do not attempt to drive other individuals from the vicinity. New birds are readily accepted in the flock although they may be relegated to a low position in the dominance order (Odum, 1941).

R. C. Miller (1921, 1922) has described the flock behavior of the Coast Bush-tit. (*Psaltriparus m. minimus*). Flocks of this species apparently have a loose organization very similar to that of chickadee flocks, although Bush-tit flocks are larger—up to 70 individuals. The behavior of Bush-tits when attacked by a hawk is quite similar to that of chickadees; the notes uttered by the Bush-tits, which Miller calls the 'confusion chorus,' corresponds to the 'warning' call described above.

Movements of the flock.—As previously indicated, flocks were followed in the field and their movements plotted on base maps. A study of sixteen such maps (each map representing an observation period of two hours to all day, averaging four hours and totaling 63 hours) involving movements of natural autumn and winter flocks (no feeding stations present) brings out the following (the figures given represent the movement of the flock as a whole as measured from field maps and not movement of individuals):

1. The average rate of movement of chickadee flocks was 1425 feet per hour (about one-quarter mile per hour). Movement, however, was not uniform but more or less rhythmic; periods of fairly rapid movement (one-half to three or four miles per hour) with little feeding were alternated with periods of little or no movement when birds were actively feeding. Active feeding periods varied from three to thirty minutes; active moving periods were generally of short duration, two to ten minutes.

2. The rate of progression was generally greater in the morning than in the middle of the day. Flocks definitely moved slowest on cold and especially very windy days (600 to 1000 feet per hour) and fastest on warm, cloudy days (2000 to 2700 feet per hour).

3. The average rate of movement between August 28 and September 13 (24 hours observation) was 1042 feet per hour; between October 10 and November 2 (23 hours observation), 2037 feet per hour; and between December 11 and January 31 (15 hours observation), 1482 feet per hour.

4. Chickadee flocks did not move in any one direction for very long but tended to double back and forth in an irregular manner and consequently to restrict themselves to an area of fairly definite limits, especially in winter.

5. No regular routes were followed by the flock in the movements over an area as Butts (1931) noted, but there were favorite feeding places (such as a hemlock tree loaded with cones) which were visited repeatedly. Thus, some parts of the feeding range and certain routes were utilized more often than others.

The three all-day observations summarized below are of special interest. On each of the three days a flock in the same area (vicinity of range 8 in Text-figure 3) was followed from 'roost to roost.'

<i>Date</i>	<i>September 13</i>	<i>October 26</i>	<i>January 31</i>
Weather	Clear	Cloudy	Cloudy
Temperature (F.)	65-75°	56-62°	15-26°
Number chickadees	9±	10±	11±
Number other birds regularly associated	20±	15±	0
Movement of flock in feet per hour	1087	2037	1744
Total area covered by flock in acres	9.3	34.9	24.2

From these data it would seem that the rate of movement of the flock was roughly proportional to the area covered. If so, the cruising range of the flock tended to be greatest during the population peak

of October, and greater in winter than in early autumn. This was also correlated with seasonal variation in habitat selection. Late-summer flocks generally remained in the woods, while October flocks were observed in all parts of the study area, even invading the abandoned weed-covered fields. In winter, birds occurred in a wider variety of habitats than in summer but not to such an extent as in the autumn. In the all-day observations the flock on October 26 spent about a third of the time in the fields and hedgerows to the east of the woods, whereas on the two other days the flock ranged entirely within the forest and forest edge.

Interspecific relations.—Little attempt seems to have been made to determine whether the commonly encountered mixtures of chickadees and other species are true flocks,—birds held together by social bonds,—or merely congregations resulting from similar habitat or food attractions (see Wing, 1941). Butts (1931) states that the association of chickadees with nuthatches and other species is a temporary one, but his statement applies only to the winter season at Ithaca, New York. Van Deventer (1936) observed two or more of four species—Chickadee, White-breasted Nuthatch, Downy Woodpecker, and Tree Sparrow—associated 31% of the time or more than could be accounted for by chance, but this association seemed to be primarily the result of habitat since all four were partial to the forest edge.

In following the chickadee flocks, special attention was paid to the associated species. If individuals of other species remained with chickadees constantly as the latter moved from place to place or from habitat to habitat they were judged to be a true part of the flock. If, however, other birds readily separated from chickadees they were judged to be largely independent. Using this criterion, the following generalizations can be made from observations in this particular locality. First, chickadees did form true, even though more or less temporary, flocks with certain species, chiefly transient warblers, vireos, and Ruby-crowned Kinglets in the autumn (and to a slight extent in the spring). Individuals of these species were closely associated with chickadees and remained with them throughout their movements. Secondly, other species were frequently associated in varying degrees with chickadees during autumn and winter, but not generally on a true flocking basis. To illustrate more specifically, species or species-groups are listed below in the approximate order of their tendency to flock with chickadees:

1. Arboreal warblers and vireos (particularly transients).—Chickadee-warbler flocks were a characteristic feature of the woods during

August and September. These flocks were often large, up to 50 or 100 individuals, which moved as a loose but definite unit. Chickadees as a species were definitely the leaders since warblers followed them rather than vice versa; the chickadees were much the noisiest and by their vocal signals seem to control the flock. Mayfield (1937) recounts a similar observation in middle Tennessee where Carolina Chickadees and Tufted Titmice share in the leadership of mixed autumnal flocks and determine the area to be covered and the rate of travel. Warblers and vireos react quickly to many of the chickadee's signals particularly the warning 'freeze' call. Many times attacks by accipitrine hawks were observed to fail completely because the warning calls of alert chickadees instantly 'froze' the entire flock before the hawk could get within striking distance. Undoubtedly, having chickadees as local escorts is of survival value to the transient warblers.

The way in which the chickadee-warbler flocks may form was dramatically illustrated by actions observed on September 13. Before dawn the contact or recognition calls of numerous warblers were heard just above the treetops, as the birds were evidently coming in from a nocturnal migration flight. For about an hour after dawn, warblers were observed all over the thirty-acre tract of wood; the birds were moving rapidly through the treetops and were calling loudly. A little later in the morning, however, the situation was entirely different; all the warblers had joined one or the other of the two chickadee flocks in the woods and were now largely silent.

Species of warblers most commonly flocking with chickadees were: Chestnut-sided, Magnolia, Black-throated Green, Black-throated Blue, Blackburnian, Canada, Redstart, Black and White, Black-poll, Bay-breasted, and several less common species. Red-eyed and Blue-headed Vireos also were strongly associated. Terrestrial warblers such as Oven-birds and Water-Thrushes did not flock with chickadees. Also, Myrtle Warblers, passing through later, were largely independent, tending to form their own flocks in more open habitat. Immature warblers began following chickadees when the first flocks formed in July. It is interesting to note that a family of Black-throated Green Warblers, in which parents were still feeding the young in August, failed to join chickadees but remained within a much smaller area.

2. Ruby-crowned Kinglet:—In October and early November, after most of the arboreal warblers had departed, the Ruby-crowned Kinglet replaced them as constant companions of chickadees. Although generally not so numerous as warblers, kinglets followed chickadees

almost as closely, and were even observed to roost in the same evergreens.

3. Red-breasted Nuthatch:—This species showed a strong tendency to flock with chickadees, but the association was limited by a still stronger habitat-preference since this nuthatch is very partial to coniferous woods. Thus, as long as chickadees remained in hemlock woods the Red-breasted Nuthatches flocked with them, but when chickadees passed into open territory or deciduous woods the nuthatches did not follow.

4. White-breasted Nuthatch:—These nuthatches exhibited a moderate degree of sociability with chickadees, sometimes following flocks for a considerable time but as often as not separating from the flocks and feeding alone or in pairs. As Butts (1931) pointed out, this species is likely to have its own customary feeding range independent of that of chickadees.

5. Golden-crowned Kinglet:—While this species was frequently observed with chickadees it usually formed its own small flocks which moved independently. On October 28, November 3, and November 6, Golden-crowned Kinglet flocks were followed instead of chickadee flocks. Several times during these observations chickadee and kinglet flocks met, intermingled for a short time, and then continued in different directions, neither flock having any effect on the movement of the other. Kinglets, like chickadees, were continually vocal and had their own contact, 'lost,' and warning notes. Like the Red-breasted Nuthatch, kinglets are also partial to conifers, and where evergreens were available the flock remained in this habitat. This species also moved at a considerably slower rate than chickadees, and the flock tended to be more compact.

6. Brown Creeper:—The status of this species was hard to determine since it was difficult to follow in the woods and was never very common. In general, however, creepers were prone to follow Golden-crowned Kinglet flocks rather than chickadee flocks. Thus, in the above observations, creepers were continually present with the kinglets and did not separate to follow chickadees when the latter passed by. This is perhaps only to be expected since the creeper's notes are very similar to those of the kinglet.

7. Woodpeckers:—Downy and Hairy Woodpeckers as well as other species were the least sociable of the small forest species; individuals generally moved about independently and rarely remained with a chickadee flock for any length of time. Transient Flickers were somewhat gregarious but entirely independent of chickadees,

while transient Yellow-bellied Sapsuckers were slightly more sociable.

8. Juncos, Tree Sparrows, and other fringillids:—Flocks of these species often fed in the same vicinity (forest edge, for example) with chickadees but were entirely independent in their movements. Here association seems to be largely if not entirely a matter of overlapping habitat choice.

Feeding and other activities.—Feeding is the principal diurnal activity of individuals in the autumn and winter flock. Other activities include: resting, preening, drinking, bathing, avoidance or scolding of enemies, general vocalization, dominance reactions, and movements from one place to another. In cold weather nearly all energy is spent in seeking food; in warm weather a proportionally larger time is devoted to other activities.

According to Forbush (1929) the food of the chickadee as shown by stomach analysis at various seasons is 68% animal (mostly small insects) and 32% vegetable (including seeds and fruit). Although no stomachs were examined during this study, a few field observations may be of interest. Chickadees are very versatile in seeking food, foraging from the ground to the tops of trees in a variety of habitats, although generally feeding at low or intermediate levels in trees and shrubs. Van Deventer (1936) found that winter chickadees were more often observed between 0 and 10 feet than at any other 10-foot horizontal level. Considering the year as a whole, five main types or methods of feeding were observed as follows:

1. Foliage examination:—Much of the insect food during the open season (spring, summer, and autumn) was obtained from both broad-leaved and coniferous foliage, and apparently some food was obtained from the latter in winter. Birds were especially fond of examining and tearing open bunches of dead leaves, cocoons, or the hiding-places of leaf-folding and leaf-rolling larvae; frequently, birds could be located by the crunching sound accompanying this activity. Large, soft-bodied green caterpillars of unidentified species were favorites during the nesting season and were frequently brought to the young. The forest tent caterpillar (*Malacosoma disstria*), periodically abundant in the region, was avoided. However, birds were several times observed to eat large woolly caterpillars (probably *Isia isabella*); the soft insides were deftly removed and the hairy outer covering was discarded. In the spring, individuals spent much time examining the opening buds and catkins of deciduous trees, especially aspen and willow; as nearly as could be determined animal rather than vegetable food was being sought.

2. Twig and bark examination:—Observed at all times of year, but most often in winter. In this type of feeding the 'acrobatic' ability of the chickadee comes into play. In addition to gleaning small insects from in and under bark of twigs, limbs, and trunks, birds were adept at locating and catching tree-trunk moths despite the latter's protective coloration.

3. Seeds and fruits:—Hemlocks (*Tsuga canadensis*) bore a large seed crop in 1939–40 and hemlock seeds were a large item in the autumnal and winter diet, perhaps more than average. In several observation periods the flock spent as much as half the time feeding on this item alone. Seeds were removed directly from the cone as birds hung upside down or sometimes the entire cone was removed and held by the feet. Birds also spent much time and energy storing seeds in cracks and crevices during the fall. Storing activity was first noted on October 12 and continued into November. On October 25, one bird made sixteen trips in six minutes between a hemlock and a yellow birch, storing seeds in the loose bark of the latter. After December no storing was observed under natural feeding conditions although birds continued to feed on hemlock seeds. I was not able to determine whether birds later returned to their caches.

Other fruits of trees and shrubs which were eaten include the following: staghorn sumac (*Rhus typhina*), yew (*Taxus canadensis*), thorn apple (*Crataegus* sp.), black alder (*Ilex verticillata*), and bird cherry (*Prunus pennsylvanica*).

4. 'Weed' top examination:—This type was restricted largely to October and November when birds invaded fields and field borders. It was rather surprising to observe chickadees clinging to the tops of goldenrods (*Solidago juncea* and *S. graminifolia*), asters, and other Compositae much in the manner of small finches. Birds not only fed on the seeds of these herbs but also skillfully picked open the stems and removed insect larvae from within. During several observation periods birds spent as much as a third of the time feeding in this way (as in the case of the all-day observation of October 26).

5. Ground feeding:—Not a small part of the chickadee's food was obtained from or near the ground although birds seldom remained on the ground very long at a time. Generally, they flew down to the ground momentarily to pick up a seed or insect, returning to a low limb to eat it. In winter, birds were often observed hopping on the surface of the snow, picking up hemlock or other seeds which had fallen from trees above.

Chickadees bathed and drank frequently in the numerous small

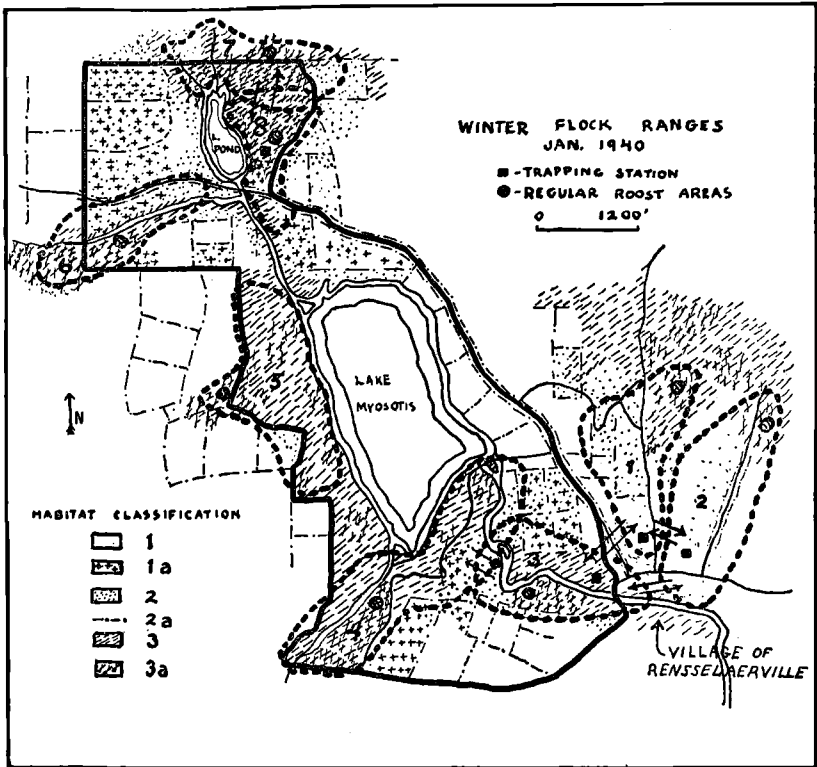
streams of the area during the autumn. Imitation was noticeable here since usually not one but several birds in the flock would fly down to drink or bathe. In winter, when everything was frozen over, what appeared to be 'snow bathing' was observed. Birds would fly down to where the sun shone on the snow and wriggle around on the moist surface. Also, birds were twice observed eating snow, presumably obtaining water in this way.

ROOSTING HABITS

Autumn and winter.—In autumn and winter most individuals roosted in dense conifer branches rather than in cavities. However, during the winter two cavities were discovered where single birds spent the night. One was a natural cavity about ten feet up in a small beech, the other an old woodpecker hole in the top of a twenty foot dead ash. On January 29, at the beech cavity the roosting bird was observed to drop out of a flock and enter the cavity very quickly; the other birds continued on to a group of hemlocks nearby, going to roost in the upper branches. Neither of the roosting cavities was subsequently used as a nesting cavity. Mogall (1939) found that Great and Blue Tits commonly roosted singly in nesting boxes during winter in Germany. Williams (1941) found Chestnut-backed Chickadees (*Penthestes rufescens*) roosting singly under eaves of houses and in vines, and quotes Bassett as reporting a Mountain Chickadee (*P. gambeli*) roosting in an old Robin's nest. Thus, while roosting habits of Paridae seem to vary in different regions, a definite tendency to roost singly and to select a sheltered place is indicated by these scattered observations.

Despite this individualism in roosting, there was a definite tendency for chickadee flocks on the Huyck Preserve to roost in the same section of woods or group of trees each night, especially in winter. Therefore, it was possible to station oneself at a known roosting area and observe the birds coming to roost. Commonly, the flock would feed up to a few minutes before roosting time; then individuals would give the flight note and start towards the roosting place. As a result, the flock was often strung out so that the birds arrived at the roosting area a few at a time, and each quickly sought out a place in densest foliage, especially out near ends of limbs. Usually only the contact and flight notes were given, sometimes a few songs. Within ten minutes or less after the first birds arrive all birds may be settled for the night sometimes at widely scattered points in the area. Calling stops as soon as the birds stop moving about which makes it very difficult to locate the exact roosting spot of individuals.

In the morning, loud chickadee calls are given which act as a general signal for individuals to leave their scattered roosting places and re-form into a flock.



TEXT-FIGURE 3.—Winter feeding ranges of flocks in January, 1940 (compare with Text-figure 1—Auk, 58: 316, July, 1941). The boundary of the Edmund Niles Huyck Preserve is indicated by the heavy solid line, the Village of Rensselaerville lying to the east. Heavy dotted lines mark the boundaries within which a group of birds was generally restricted. Arrows indicate known cases where birds passed from one flock to another. The habitat classification is as follows: (1) abandoned fields, herb and shrub stage; (1a) abandoned fields, artificially planted in conifers 10–13 years ago; (2) young forests or “second growths”; (2a) hedgerows; (3) mature, primarily deciduous forests; (3a) mature, primarily coniferous forests (hemlock, hemlock-beech, hemlock-white pine, hemlock-birch, etc.).

During the autumn, birds frequently roosted in low conifers, such as the pine plantations on the Preserve (Text-figure 3). While it was rarely possible to observe individual birds actually select a roosting spot, so quickly and completely did they hide them-

selves, it was possible to dislodge the birds from the low branches after dark, proving that they were roosting there. Five such low roosting places were located during October and November, three of which were known to be used on successive nights. During the winter, however, these low places were abandoned and birds roosted mostly in tall hemlocks, pines, or spruces (planted). The location of the regular roosting places used by winter flocks is shown in Text-figure 3.

Location of roosting areas seems to have possibilities as a method of censusing, especially during the winter fixation period. At least estimates by this method checked well with estimates based on banding and location of flocks in the daytime.

Breeding season.—As the flocks break up and pairs separate out or form in the spring, the winter roosting places were abandoned. During the pre-nesting movements the pair seemed to roost wherever it was convenient. The sexes were not observed to roost close together like Wren-tits (Erickson, 1938); in two out of three observations they did not even roost in the same tree, as may be seen by the following observation:

April 15. Pair no. 5. 5:49 p. m. Male flew up from a low bush where he had been feeding, called *chickadee*, flew across an opening into the top of a thirty-foot hemlock located in the middle of an isolated clump of trees. With aid of field glasses able to see bird perched on a small twig and nearly hidden by dense foliage. Here the male remained motionless as night came on but did not immediately assume characteristic roosting pose (head buried in scapular feathers). In the meantime (5:51 p. m.) the female had disappeared. Going over to where she was last seen I flushed her from a low branch of another hemlock. After scolding she worked out along another limb and roosted near the end about eight feet up. Returning later with a flashlight I was able to locate her in same place. Thus, members of the pair roosted 150 feet apart in different hemlocks.

As previously described (part 2) the female roosted in the nesting cavity from the time it was completed until the young were well developed. The male always roosted elsewhere; in one case he roosted in a small maple near the cavity on two successive nights and could be observed with a flashlight. After the young left the nest the family roosted wherever they happened to be. Likewise roosting places in late summer seemed to be more or less temporary although only a few observations were made.

Time of roosting.—The roosting time of the flock was recorded as the time when the last call was heard; by that time all birds were usually settled in roosting places. Observations of roosting time of flocks in relation to sunset (data obtained from the 'World

Almanac,' with corrections for Rensselaerville latitude) are summarized below. *Plus* figures indicate number of minutes *before* sunset; *minus* figures, minutes *after* sunset:

	October	December	January	February	March
Total observations:	6	2	14	4	3
Average	-7 min.	+3 min.	+23 min.	+20 min.	+35 min.
Variation	+1 to -12	+9 to -4	+40 to +5	+29 to +15	+48 to +25
Clear days:					
No. observations	3	1	6	3	0
Average	-10	+9	+20	+18	-
Partly cloudy days:					
No. observations	0	1	3	1	2
Average	-	-4	+19	+23	+28
Very cloudy or snowing:					
No. observations	2	0	4	0	1
Average	-1	-	+26	-	+48

A few observations on the time of roosting of pairs or single birds during the nesting season may be summarized as follows:

	Female	Male	Remarks
April 16	+50 min.	+49 min.	Pair 5, both in evergreens
April 27	+27	+27	Pair 1, both in evergreens
*May 13	+71	+62	Pair 1, before egg laying
*June 4	+29	+16	Pair 3, egg-laying period
*June 5	+43	+17	Pair 3, egg-laying period
*Aug. 3	+17	?	Pair 16, feeding young
*Aug. 5	+17	?	Pair 16, feeding young
*Aug. 8	+16	+8	Pair 16, feeding young
*Aug. 9	-1	?	Pair 16, feeding young

*Female roosting in cavity, male roosting elsewhere.

Despite the small number and considerable variability of these two sets of observations several interesting things are indicated (which, however, need to be checked by further observations): (1) Roosting time varied with the season; flocks roosted later in relation to sunset during October than during the winter months, and apparently individuals tended to roost earlier in April and May than in the summer. (2) Birds roosted earlier on cloudy and especially snowy days than on clear ones. (3) With the beginning of cavity roosting during nesting the female of the pair retired first, the male sometimes continuing to feed for some time after the female had entered the cavity for the night.

Seasonal variation in roosting time in relation to sunset has been indicated for the European Tree Creeper (*Certhia familiaris britannica*) (Rankin and Rankin, 1940), Chestnut-backed Chickadee

and Bewick's Wren (*Thryomanes bewicki*) (Williams, 1941). Nice (1939) found that the awakening song of the Song Sparrow was influenced by the time of year since it varied somewhat from the sunrise curve, tending to follow more closely the curve for civil twilight. The Tree Creeper roosted earlier (in relation to sunset) in spring than in December and January, similar to the trend in the above data. Williams (1941) found a similar sex difference in roosting of the Chestnut-backed Chickadee, the female roosting earlier and arising later than the male. Williams also found some evidence to show that weather affects roosting time independently of light intensity since birds roosted at relatively high light intensities on rainy days. Allard (1937) comments that many species seem to begin singing or other activity promptly at certain times in morning but do not seem to end singing or other activity with quite the same regularity.

A few observations were made on the time of leaving roosts in the morning. Two observations in October averaged two minutes before sunrise and three observations in January averaged six minutes before sunrise. Compared to many other small birds, chickadees are early to roost and late to arise. In winter, Tree Sparrows were regularly active and feeding one-half to three-quarters of an hour after chickadees had roosted. Likewise, Tree Sparrows and Pine Grosbeaks were observed coming from roosts a half-hour or more before chickadees in the morning. In the summer, such birds as thrushes and Song and Field Sparrows sang long after chickadees had roosted and become silent. Thus, in October chickadees spent about 13 hours on the roost, and in January between 14 and 15 hours. This long period is of special physiological interest since it means that the birds must be able to tolerate a long period without food at the low temperature of the winter season. Williams (1941) found that Chestnut-backed Chickadees spent more time on the roost than Bewick Wrens (from thirty minutes to one hour and fifteen minutes longer); the chickadees consistently roosted before sunset, the wrens after sunset.

Roosting chickadees have been observed closely both in captivity and in the field. In all cases the head was turned back over the shoulder and the bill buried in the feathers of the scapular region. Except at high temperatures (under experimental conditions) the feathers were fluffed out so that the roosting bird resembled a fluffy ball with a black stripe across one end and a tail protruding from the other.

DOMINANCE RELATIONS

The 'peck-order' or social organization of bird flocks has been intensively studied in flocks of domestic or caged birds (see Allee, 1936) but little study has been made with wild flocks. The dominance relations within one of the village flocks were studied in detail during the winter and early spring, and occasional observations made on other flocks. About thirteen birds regularly visited the feeding station with others appearing from time to time, especially in the spring. When feeding away from the station the birds traveled as a flock or as two or more flocks. Behavior of each individual in relation to every other individual was observed at the feeding station and also under natural feeding conditions where contacts were less frequent. Three criteria of dominance were used: (1) actual fighting, (2) bluffs, threats (with open bill), or use of the dominance note, (3) withdrawal of the bird at the approach of another (hence indicating subordination). The last criterion was applied only in clear-cut cases and was used mainly to supplement the other two criteria. About 600 dominance reactions between the color-banded individuals were recorded between January 15 and April 15.

There was a definite dominance order in the flock studied. Individual A-RG, male, was the top bird dominating all others. A-RY, male, was next, dominating all birds except A-RG during the winter, although this individual yielded the second place to A-GR, also male, in late February and March (see below). Likewise, A-Y, sex unknown, was clearly at the bottom of the winter group being displaced readily and frequently by every other bird. A-GY, sex unknown, dominated only A-Y, while A-B1, female, dominated only A-Y and A-GY. However, the dominance order was not entirely linear nor definitely fixed. Dominance was not clearly established between some of the intermediate birds, one individual being dominant one day or in one situation and the other being dominant another day or in another situation. There was some indication of a triangle relationship between three of the intermediate birds. Where dominance was clearly established, the subordinate bird usually withdrew without argument when the dominant bird approached, threatened with open bill, or gave the dominance note (often all three happened simultaneously). Since the subordinate bird was usually quick to get out of the way, no blow was actually passed in such cases. Actual fighting, therefore, took place mostly between closely ranked birds. On the other hand, contacts between certain closely ranked individuals were few, the two birds seemingly having a mutual respect for each

other and avoiding contacts. Displacements were most frequent between the top four or five birds and the bottom four or five.

In the group of thirteen birds there was a possibility of 78 different inter-individual contacts. Of the 78, 54 were (as far as observed) always in the same direction; that is, one bird was able to chase the other. In 18 cases the situation was one of give and take, with first one and then the other individual winning out. In six cases there were little or no data. Thus, this social hierarchy of chickadees resembled the 'peck right' system of the domestic fowl in the case of most individuals, and the 'peck dominance' type in the case of some of the intermediate or closely ranked birds. In other words the 'peck-order' seemed to be fairly rigid but not absolutely so.

On the whole, the dominance order changed very little during the winter and early spring. A-GR, mentioned above, was, however, a notable exception. In January, this individual was low ranking, avoided contacts and was even dominated by A-B1, female. During February, he became more aggressive, gradually improving his status until by March he was ranked as no. 2, chasing all birds except A-RG, the 'kingpin.'

Birds which visited the station occasionally from the two neighboring flocks were, without exception, relegated to a low position in the dominance order. One visitor, however, worked up to a high position after several visits. The three birds which joined the flock in March remained in a low position, being dominated by all but the lowest two or three birds. One of these spring arrivals proved to be a female and eventually mated with the no. 1 bird. A similar situation in regard to newcomers was observed when birds were experimentally transferred from one flock to another (Odum, 1941).

Dominance reactions were not restricted to feeding stations, although contacts were less frequently observed in loose flock formations under natural conditions. Displacement, chasing, use of 'dominance note,' and occasionally a fight were observed, similar to those on the feeding shelf. Chasing and fighting were especially vigorous among immatures in the late summer and autumn flocks. Here fighting was often clearly not over food, indicating that establishment of dominance is a fundamental social trait not necessarily associated with feeding. With the constantly changing population of autumn it is probable that dominance relations are continually being worked out and that a fixed system does not develop until the winter fixation period.

Mrs. Hamerstrom (1942) independently has made a study of

dominance in winter chickadees in Wisconsin, also finding that relations were generally unilateral. Her results, however, indicated an even more despotic type of social order than mine. This difference may be due to her smaller number of observations and the fact that she used only actual fighting as a criterion which, it seems to me, overlooks many interesting dominance reactions where an attack by one bird is not opposed by another resulting in a definite displacement but not in a fight. Of 76 fights observed by Mrs. Hamerstrom only one reversal was noted. According to Allee (1938) the only bird so far studied in his laboratory which has a fixed dominance order approaching that of the fowl is the White-throated Sparrow (*Zonotrichia albicollis*) recently reported on by Wessel and Leigh (1941). In flocks of three to five of this species the social order was a straight-line type; with larger flocks triangles developed. It is interesting to note that the White-throat, like the chickadee, flocks but loosely. Likewise, observations by Tompkins (1933) on several species of winter birds in California indicated that the most solitary species, a San Francisco Towhee (*Pipilo maculatus falcifer*), had the most rigid dominance relations. The social hierarchy of most birds which have been closely studied—i. e., canaries, pigeons, parakeets—is not fixed ('peck-dominance' type). These later species, theoretically at least, tend to flock more closely. This suggests that there may be important relations between the type of social order and the type of flock under natural conditions.

To sum up, dominance would seem to be important in at least four ways in wild-chickadee groups although much more study is needed. First, as indicated above, males were usually but not always dominant over females. In the case of pairs which formed from these and other flocks, the male was strongly dominant over the female while the two were in the flock. Hence dominance is probably involved in pairing. Secondly, as already indicated in an earlier part of this paper, the three top males were the ones that remained on or near the winter feeding range to establish territory and nest, indicating as Shoemaker (1939) has shown that social dominance and territory are related. Thirdly, dominance may play a role in winter survival. Certainly dominant birds had the advantage at the feeding station because low-ranking birds were forced to make more trips to the station since their feeding was often interrupted. However, whether this is of any importance under natural feeding conditions is a question (see Hamerstrom, 1942). Finally, as previously suggested, the type of dominance order may have something to do with the char-

acteristic loose organization of chickadee flocks. This is perhaps the most interesting and significant possibility and should be investigated further.

WINTER DISTRIBUTION

The winter feeding ranges¹ of the eight more or less well-defined flocks as of January 1940, are shown in Text-figure 3. The locations of regular trapping-stations and flock-roosting areas are also shown. The map is drawn to the same scale as Text-figure 1 (see part one). The area within which a group of birds were regularly restricted is indicated by the heavy broken lines. Several ranges overlapped to an appreciable extent. As previously pointed out, winter flocks were not entirely stable; some individuals ranged farther than others or were inclined to pass from one group to another. Arrows indicate known cases where individuals passed from one flock to another. Nevertheless, flocks were often remarkably restricted in their movements and constant in individual composition, as Wallace (1941) found at Lenox, Massachusetts. Thus, although feeding stations in flock ranges 1, 2, and 3 were only 200 to 300 yards apart, only four or five birds out of about forty visited more than one station since the flocks generally ranged in different directions. Experiments in winter homing previously reported (Odum, 1941) showed that many individuals returned promptly to winter areas when removed short distances (birds were transferred from ranges 1 and 2 to range 8) while others did not return and a few even remained at the point of release.

The size of these winter areas as drawn in Text-figure 3 varies from 21.8 acres to 55.8 acres, averaging 36.1 acres (approximately 14.6 hectares). Butts (1931) estimated one winter range to be about 40 acres. The number of birds using these areas varied from twelve to fifteen in the village and in ranges 6, 7, or 8 to but five or six in ranges nos. 4 and 5. Birds were, therefore, concentrated in the village and in the extensive hemlock and beech-hemlock stands around Lincoln Pond.

Consideration of the winter fixation period brings us to the end of one complete year since the paper started with spring movements and pair-formation. Of the total banded population present in late February, 18% remained on or near the winter feeding range to nest, 29% moved to other parts of the study area, and 53% disappeared, apparently moving out of the study area.

¹"Winter territory" is used by some authors but since the winter areas are not defended, "feeding range" is preferable.

RESUMÉ OF THE ANNUAL CYCLE

Considering the annual cycle as a whole, the behavior of the chickadees resolves itself into six major seasonal patterns. These correspond well with the six seasons—prevernal, vernal, estival, serotinal, autumnal, and hiemal—which animal ecologists have proposed for the classification of aspection phenomena in temperate climates. Therefore, while I am aware of the shortcomings of any attempt to pigeonhole what in Nature are continuous or overlapping events, it may be instructive to review very briefly the chickadee's year in six parts as follows:

1. *Prevernal period* (March).—Spring movements, characterized by increasing restlessness and singing, shifting of birds from one flock to another, appearance of new birds and disappearance of others. In 1940, this period was delayed and prolonged into April by unseasonable weather.

2. *Vernal period* (April).—Preliminaries to actual reproduction including gradual breaking up of flocks and dispersal of individuals or pairs, pair-formation apparently resulting from simplified courtship, beginning of territory establishment following rather than preceding pair-formation.

3. *Estival period* (May–June).—Period of actual nesting in which most individuals are paired, remain in and defend territories. The sexes cooperate closely in all the nesting activities although only the female carries in nesting material and incubates. The male aids in cavity excavation, feeds the female during egg laying and incubation and takes an equal or greater share in feeding the young. The incubation period is about 13 days, the young remain in nest 16–17 days and remain a month or less with parents after leaving. This period was prolonged by a second brood or second nesting attempts in the case of some pairs.

4. *Serotinal period* (July–August).—Characterized by movement and flocking of juveniles and the molting of adults. The flocking habits reappear and the woods become 'alive' with noisy roving flocks. The family group does not form the basis of the flocks since juveniles scatter widely while adults remain for the time being on or near former nesting territories.

5. *Autumnal period* (September–November).—Characterized by autumnal movements, high population, mixed flocks, and general high sociability. Juveniles apparently may move long distances, adults short distances, but more data are needed. Transient warblers, vireos, and Ruby-crowned Kinglets consistently flock with chickadees; other

species are less strongly associated. This is probably the most 'care-free' period in the chickadee's year since nesting and molting are over and temperatures have not yet become low enough to make the business of living critical. On the other hand, judging from the frequency of observed attacks, the danger from accipitrine hawks is probably greatest at this time.

6. *Hiemal period* (December–February).—Winter fixation period, when most individuals remain within restricted areas of 20 to 50 or more acres and associate in small flocks. Apparently, well-defined dominance orders may develop in winter flocks. Feeding is the most important activity, and concentrated food, whether natural or artificial, may influence habits and distribution. Despite the rigors of the winter climate the study area maintained more birds at this season than during the estival period.

SUMMARY

(Part 1)

1. A study of the Black-capped Chickadee (*Penthestes atricapillus atricapillus*) during one complete year was made on the Edmund Niles Huyck Preserve, Rensselaerville, New York, and adjoining areas during 1939–40. The present paper summarizes results of the field study.

2. Colored bands in addition to numbered ones were used to permit exact individual recognition in the field. Birds were banded during the winter and spring at feeding stations; other adults and nestlings were banded at the nests, all of which were located in natural situations.

3. All observations were made within a two-mile diameter with the most intensive study carried on within the 476-acre Preserve and 100 acres of the adjoining village of Rensselaerville. The study area is located on the Helderberg peneplain at an elevation of 1400 to 1700 feet, ecologically lying in the ecotone between northern coniferous and eastern deciduous forest biomes. A wide variety of habitats ranging from abandoned fields to young beech-hemlock climax is present.

4. Chickadee population on the study areas experienced considerable seasonal variation. A peak of approximately thirty birds per 100 acres was reached on the Preserve in the fall, while a similar peak was reached in the village during the winter. Population was greater in winter than during the nesting season in both areas, the ratio being 15 to 6 on the Preserve and 30 to 4 in the village vicinity.

5. Unlike the way with many passerines, courtship and mating take place before the establishment of a definite nesting territory which may or may not be established at the place where pairing occurred.

6. Little evidence was found for the existence of definite pairs in the winter flocks, although pairs remained together after nesting. Published banding evidence indicates that chickadees (and many other Paridae) may retain the same mates in successive seasons, mortality permitting, but apparently the bond (if any) between the pair is ill-defined during the winter flocking period.

7. The break-up of winter flocks was gradual with pairs or single birds separating out a few at a time. Not more than two pairs remained to nest on any one winter range and one range was evacuated completely. Some birds were followed or later located within a mile of winter areas but many (about 53%) disappeared, apparently moving a greater distance.

8. No clear-cut courtship ritual was observed; courtship is apparently simple, although perhaps prolonged, involving use of loud *phoebe* songs by the male, a special twittering mating note, and wing-fluttering ceremonies.

9. Begging by the female and feeding of the female by the male are apparently not a part of courtship in chickadees since this behavior was not observed until later, particularly during incubation.

10. Behavior of birds which lost mates was described. A new mate is readily accepted when one is lost. One female had three mates during the nesting season. No cases of polygamy were encountered.

11. Establishment and defense of a definite nesting territory begins about the time of cavity excavation and ends when the young leave the nest; the finding of a suitable nesting site is probably an important factor. The male assumes the leading rôle in territory defense which follows three steps: vocal challenging, chasing, and rarely actual fighting. Observations are interpreted as indicating that 'fighting' for the mate gradually changes to 'fighting' for territory.

12. Where there is contact with neighbors the territorial boundaries may be sharply marked out; otherwise boundaries are not rigidly fixed.

13. Territories at maximum size patrolled, varied from 8.4 to 17.1 acres, averaging 13.2 acres (5.3 hectares). The size of territory and the vigor of its defense decreased as nesting progressed.

14. Two distinct habitats, an early seral and a late seral vegetation stage, were often included in a territory correlated with requirements for nest site on one hand and feeding-resting places on the other.

(Part 2)

15. Both sexes working in close coördination excavate the nesting cavity, although the female apparently takes the lead; chips are carried a short distance away. The pair work intermittently throughout the

day spending the inattentive periods in other parts of the territory.

16. The depth of cavities varied from 5 to 6.25 inches and the inside diameter from 2.5 to 2.75 inches; entrances were variable. Well-decayed stubs of early successional trees were most often selected.

17. Hair of the cottontail (*Sylvilagus floridanus*) was conspicuous in all seven nests examined; other hair, plant down, thin bark and strings were also used.

18. The number of eggs varied from five to eight, with four out of seven sets having seven eggs. Eggs are laid one a day and covered with nesting material by the female; the female spends the night in the cavity before and during egg laying, but apparently does not begin incubating until the set nears completion.

19. Contrary to a few standard references, no evidence was found to indicate that the male incubates; only the female developed a brood-patch and incubated, although the male often came to the nest to feed the female.

20. The average attentive period of three females was 24 minutes, the average inattentive period, 7.8 minutes. The male announces his approach to the nest with a signal song. During the inattentive period the female begs constantly and is fed at intervals by the male; in the meantime she feeds herself. The incubation period was thirteen days in one case.

21. The behavior of adults during the first week after hatching is similar to that during incubation except that the male stops feeding the female and both feed the young. As the young increase in age the behavior of both sexes changes; brooding ceases, ceremonies are dispensed with, and both sexes behave very much alike.

22. The male fed two to four times more often than the female at first, but when brooding stopped, both sexes fed at about the same rate. Feeding advanced young places a great strain on the energy reserves of the adults so that survival time without food was found to be very low, less than 16 hours in two cases. Nestlings remain in the nest 16 to 17 days.

23. Morphological and physiological development of the nestlings is typical of altricial species. Weight increased from slightly over a gram at hatching to 9-10 grams at twelve days, with little or no increase during the remainder of nest life. Temperature control began to develop on the fourth day and by the twelfth nestlings were essentially warm-blooded. At average nest temperature (95° F.), the highest heart and breathing rates were recorded at nine days, believed to be the result of poor feather development at this age as compared with high development of the heat-production mechanism.

24. Fledglings were able to feed themselves ten days after leaving the nest and remained with their parents only three to four weeks. In late summer, adults tended to remain on or near their former territory but the juveniles scattered widely; hence, late summer flocks were not usually family groups.

25. Only one brood was attempted by most pairs although one female in 1940 and several in 1941 raised two broods.

25a. Of nests most closely watched 60% were successful, while approximately 70% of all eggs laid (including second layings) were fledged. Survival of the adults during the nesting season was 90%.

(Part 3)

26. Vocal activity is very important in regulating the behavior of chickadees, especially during the flocking period. Sixteen clearly distinguishable notes are listed, most of which have well-defined functions; eight function primarily in breeding behavior, and eight function primarily in general social relations.

27. The characteristic autumn and winter flocks are rather loose aggregations of individuals which do not move in a well-organized manner or have definite leaders. Chickadees are apparently strong individualists but at the same time have considerable social tendencies during the non-breeding season.

28. The number of individuals in natural flocks in the woods averaged seven to eight, while flocks or 'congregations' in the vicinity of village feeding stations were larger. The larger autumnal population on the Preserve resulted partly in larger flocks but mostly in more numerous flocks.

29. Flocks are not definitely fixed in size but may vary from day to day or even from hour to hour; flocks continually break up and re-form or individuals pass from one flock to another, especially in the autumn.

30. The average rate of movement of flocks was 1425 feet per hour. Movement, however, was not uniform but more or less rhythmic, periods of fairly rapid movement alternating with feeding periods in which there was little or no movement.

31. Flocks moved faster in the morning than in the middle of the day, faster on warm, cloudy days than on cold or windy days; the average rate of movement was greatest in October and greater in winter than in late summer.

33. Flocks usually did not move in any one direction for long but tended to double back and forth in an irregular manner over a fairly

definite area. No regular routes were followed, but favorite feeding places were sometimes visited repeatedly.

34. All-day observations seemed to indicate that rate of flock movement was proportional to area covered, which in turn was correlated with seasonal variation in habitat selection.

35. Arboreal warblers (particularly transients), vireos, and Ruby-crowned Kinglets consistently flocked with chickadees during late summer and autumn. Other species, such as White-breasted and Red-breasted Nuthatches, Golden-crowned Kinglets, Brown Creepers, and woodpeckers were often associated to varying degrees, but not generally on a true flocking basis.

36. Chickadees are very versatile in their feeding habits. Five main types or methods of feeding were noted as follows: (1) foliage examination (principally open seasons), (2) twig and bark examination (principally winter), (3) seeds and fruit (autumn and winter), (4) 'weed'-top examination (restricted to autumn), and (5) ground feeding (sparingly the year-round).

37. Most individuals roosted in dense conifer branches during autumn and winter, although two cavities were located where single birds roosted in winter. There was a definite tendency for flocks to roost in the same conifers on successive nights, especially in winter. In autumn, birds often roosted in low conifers, but in winter they roosted high up. While nesting, the female roosted in the nesting cavity, the male always roosted elsewhere.

38. Factors other than light intensity which apparently influence roosting time are season (birds roosted much earlier in relation to sunset in spring than in fall), weather as such, and sex (female went to roost earlier than male during nesting). Compared to many other species, chickadees are early to roost (consistently before sunset) and late to arise.

39. There was a well-defined dominance order in one of the winter flocks which was studied in detail. Dominance seemed to be well established and uni-directional between many individuals but the dominance order was not entirely linear or fixed. Males were mostly dominant over females, and newcomers or spring arrivals were relegated to a low position in the dominance order, at least at first. Under natural conditions the evidence indicates that dominance may be important in (1) mating, (2) territory, (3) winter survival (doubtful), and (4) in determining characteristic loose flock organization.

40. The winter feeding ranges of flocks were mapped on the same scale as nesting territories. Ranges varied from 21 to 55 acres, aver-

aging 36 acres (approximately 14.6 hectares). In winter, birds were concentrated in the village (where feeding stations are maintained each year) and in the extensive hemlock stands of the Preserve.

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