ANNUAL CYCLE OF THE BLACK-CAPPED CHICKADEE—1

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INTRODUCTION

A STUDY of the Black-capped Chickadee (*Penthestes atricapillus atricapillus*) during one complete annual cycle was part of the research program of the writer during 1939–40 at the Edmund Niles Huyck Preserve, Rensselaerville, New York. Because of a year-around availability and comparative tameness the chickadee is an excellent subject with which to combine field and laboratory techniques in the study of behavior and ecology. As a control for experimental work with a wild species it is desirable to be familiar with the normal life history. Also, laboratory experimentation is more intelligently carried out after the problems in behavior become clearly outlined through field observation. Despite the fact that the chickadee is a common bird many details of its life history are either not known or poorly recorded. Consequently, a study of the chickadee in Nature has been the first objective, but at the same time experiments in the laboratory were begun with the cardio-vibrometer, an instrument which measures certain physiological rates.

An attempt was made to carry on the field work with equal intensity throughout the year. Between August 28, 1939, and September 6, 1940, observations were made at least weekly and often daily, except during the last two weeks in November and December when the writer was absent from the region. However, the present report is not intended to be a complete life history of the species, but rather the result of a year's study in a restricted locality. For convenience, the annual cycle will be divided into three parts: (1) pair-formation and territory; (2) nesting; (3) flock organization and general behavior. For the most part the laboratory phase of the study will be reserved for another paper.

The writer is indebted to the officers of the Edmund Niles Huyck Preserve and to the Scientific Advisory Committee for opportunity to conduct the work. Frequent encouragements and helpful suggestions by the late Dr. G. Kingsley Noble were of inestimable value. Appreciation is also expressed to Mrs. Margaret M. Nice, Dr. Ernst Mayr, Dr. A. L. Rand, and Dr. S. C. Kendeigh for critical reading of the manuscript. Abstracts of certain European papers were kindly loaned by Mrs. Nice.

METHODS

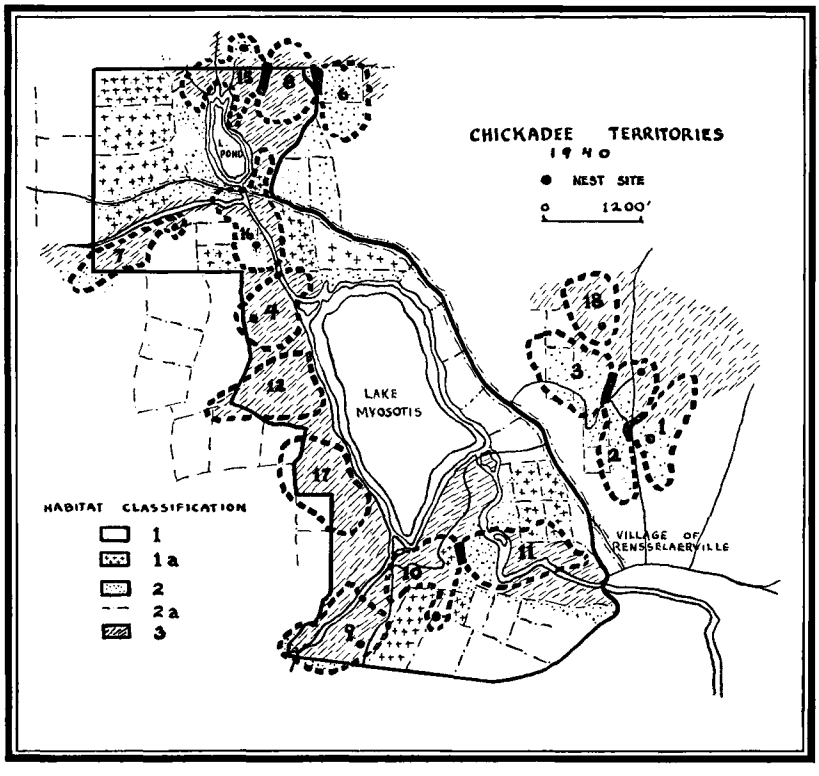
Both colored celluloid and numbered aluminum bands furnished by the Fish and Wildlife Service of the U. S. Department of the Interior were used, the former to permit individual recognition in the field. The free ends of the colored bands were firmly fastened by use of Duco household cement (acetone may also be used) eliminating any possibility of birds pulling them off or of bands slipping down over one another where two bands were placed on the same leg. Not a single case of a lost or misplaced band has yet come to my attention. Since the tarsal length of the chickadee is limited, colored bands 3 mm. in width (half-bands) were frequently used instead of the 6 mm. bands. No real difficulty was experienced in seeing even the small bands with the use of an 8-power binocular since a close approach can usually be made, especially in the vicinity of the nest.

Eighty adults were color-banded during the winter and early spring, making it possible to follow many birds from the beginning of the breeding season without disturbing them further. Several additional adults were captured for banding or examination at the nest by placing a small net over the entrance hole after the bird entered. A trap door was not needed since most individuals were not easily frightened out. Only four out of thirty birds breeding on or near the Preserve remained unbanded. Thirty-one nestlings were also color-banded in order to follow the dispersal of the young.

All nests were located in natural situations; no artificial boxes of any kind were provided since it was particularly desired to study territory, nesting habits, and population density under natural conditions. In order to observe the contents of nesting cavities a portion of the front of the cavity was frequently cut out with a small coping saw and the piece held in place by wire wrapped around the nest tree. In this way the front of the cavity could be removed easily whenever needed. In no case were the birds disturbed for more than a few minutes after the initial cutting.

The study area.—All observations of chickadees were made within an area roughly two miles in diameter. Included in this study area are the village of Rensselaerville and the Edmund Niles Huyck Preserve of 476 acres, within which the most intensive study was carried out. The region is located on the Helderberg peneplain of eastern central New York at an elevation 1400 to 1700 feet. Ecologically, it lies in the ecotone between the northern coniferous forest and the eastern deciduous forest areas or biomes (roughly equivalent to the eastern portion of the transition life-zone). A wide variety of habitats

is present ranging from recently abandoned fields through various young forests to young beech-hemlock climax, as is partially indicated by Text-figure 1.



TEXT-FIGURE 1.—Territories of chickadees in June 1940. The boundary of the Edmund Niles Huyck Preserve is indicated by heavy solid line. Chickadee territories at maximum size defended are indicated by heavy dotted lines. Solid lines between territories indicate points where actual boundary disputes were observed between adjacent pairs. The habitat classification is as follows: (1) abandoned fields, herb and shrub stages; (1a) abandoned fields, artificially planted to conifers 10–13 years ago; (2) young forests or 'second growths'; (2a) hedgerows; (3) mature forests of beech-maple, beech-hemlock, etc.

The spring of 1940 was generally late, following a severe winter in which the heaviest snowfall occurred between February 15 and March 15. Snow formed a continuous cover until April 1, while five inches of snow fell on April 13, and ten inches on April 21. Ice, generally a good seasonal indicator, did not completely leave the ponds until May 1. The break-up of winter chickadee flocks and appearance of

definite mating behavior did not take place until the period between April 10 and 25, during which maximum daily temperatures varied from 34° to 52° F.

THE CHICKADEE POPULATION

The Black-capped Chickadee is the only member of the Paridae present in the region. It is the most abundant bird species which occurs in the study area throughout the year; however, there is considerable seasonal variation in numbers and the population is not entirely resident. In 1939–40, the population on the Preserve itself was greatest and most variable in late summer and fall. The winter population was approximately fifty as compared with twenty for the breeding season. In the village (located in the valley and supplied each year with feeding stations) the winter-summer population ratio was about 40–4. Most of the breeding birds were present in winter although several moved as far as a mile from winter range to summer territory. Of thirty breeding adults (fifteen pairs) on or near the Preserve, nineteen had been banded during January and February, two during mid-March, and the winter whereabouts of nine were unknown. On the other hand some 35–40 banded birds regularly present on the study area in winter and early spring disappeared during the breeding season. Similar seasonal changes in population have been reported by Dr. George J. Wallace (1941) at Lenox, Massachusetts, and by Butts (1931) at Ithaca, New York.

PAIR-FORMATION

In life-history study the importance of the preliminaries to actual reproduction has been emphasized in recent accounts of courtship and pair-formation by Lorenz (1935), Tinbergen (1939), Noble (1939), Lack (1940), and others as well as by the development of the territory theory by Howard (1920). In most passerine birds that have been adequately studied the male first establishes a territory; courtship and mating then take place when the female enters the territory. In the chickadee, however, my observations indicate that the sexual bond is formed before and usually not in connection with the establishment of nesting territory which is defended later. Steinfatt (1938) likewise states that pair-formation in seven species of European wood titmice (including *Parus atricapillus salicarius*[1]) is not dependent on the presence of a nesting territory.

Permanence of mating.—There is considerable evidence that paired birds of many Paridae maintain an attachment for each other beyond the breeding season or may remain mated for life. Permanent mating is reported in several European species. Steinfatt (1938) found that

Marsh Tits (*Parus palustris*) wander about in winter in pairs and states that this species, the Crested Tit (*Parus cristatus*) and the Willow Tit (*Parus atricapillus salicarius*)[1] are permanent residents and mate permanently in East Prussia. Warga (1939) in fourteen years of banding Great Tits (*Parus major*) at Budapest did not record any change of mates from season to season provided both birds were alive although the birds traveled in flocks in winter. Kenrick (1940) found that Blue Tits (*Parus caeruleus*) in England were partly migratory and partly resident but that the same mates were usually retained from season to season. However, he records one case of a male mating with a female whose mate of the previous year was still alive.

In regard to the North American Paridae, Price (1936) states that the Plain Titmouse (*Baeolophus inornatus*) in California is usually seen in pairs the year around and keeps the same mate from year to year. The same may be true of the Tufted Titmouse (*Baeolophus bicolor*) (Gillespie, 1930). Nice (1932) reports a case of a pair of Carolina Chickadees (*Penthestes carolinensis*) which remained associated three winters and two summers in Ohio. In the case of the Black-capped Chickadee, Baldwin (1934) records several pairs which she believed remained mated for two or more seasons in Massachusetts. She particularly noted nesting pairs returning to the feeding station together in the fall. Butts (1931) in a two-year study at Ithaca, New York, did not record any cases of the same mates in successive years, but believed this due to disappearance of one of the pair.

While little regarding the permanency of mating can be determined in a one-year study the following observations may have some bearing on the question. Of 18 pairs followed during the spring and summer seven were formed from birds which were members of the same winter flock. The mates of two pairs were from different flocks (as much as a mile apart in one case) and one mate in each of nine pairs was not banded during the winter. Since every effort was made to band all birds wherever banding was carried on, it is fairly certain that these unbanded birds were not in the flocks with the banded birds, or at least not regularly associated with them. Thus, in about 60 per cent of the cases a paired condition could not have been maintained over the winter. Of course, mortality might account for this since the chickadee is a comparatively short-lived species. Wallace (1941) at Lenox, Massachusetts, found that the mortality from winter to winter was about 30 per cent from 1937 to 1938 and over 40 per cent from

[1] *Parus* (*Penthestes*) *atricapillus salicarius* occurring in Central Europe and *P. a. kleinschmidti* occurring in England are generally regarded as subspecies of our Black-capped Chickadee (*Penthestes atricapillus*).

1938 to 1939; he also believed that mortality over the winter of 1939–40 may have been greater than during the previous two winters. Therefore, the chances of at least one member of a pair not surviving from one breeding season to the next would be considerable.

In regard to the seven intra-flock matings there was little evidence to indicate a mated condition prior to the time the pair actually separated out from the flock in the spring. In general, no definite ties between any two individuals could be discovered in the winter flocks; no two birds tended to feed together day after day or to show by notes or behavior special attachments for each other, even though the same individuals tended to remain associated in the same flock all winter. It is quite possible that some pairs did exist within the flocks but I could discover no way of identifying them when their history during the previous breeding season was unknown. On the other hand, in early September of 1940, two known nesting pairs were observed still together although not especially closely associated in flocks otherwise composed of wandering juveniles not their own offspring.

To sum up, the scattered evidence from banding indicates that the pair in the Black-capped Chickadee and in the Paridae in general tend to remain together after the breeding season, may remain in or return to the same wintering area, and, if alive (or present in the same region), are likely to nest together the next breeding season. In the chickadee, however, which unlike certain other species (i. e. the Marsh Tit or Plain Titmouse) flocks in winter, it is not clear whether birds actually remain paired during the winter or simply remain in the same region and remate again in the spring. If pairs are maintained apparently the bond between them is very loose during the winter flocking period. Perhaps pairing in the chickadee is intermediate between the type seen in many passerine species in which the birds definitely separate after the nesting period and that of such a species as the Wren-tit (*Chamaea fasciata*) in which the pair remain very closely associated and hold a territory throughout the year (Erickson, 1938).

Courtship and mating.—The first evidence of courtship and definite breeding pairs, as already mentioned, did not take place this year until the period of April 10–25. Prior to this in late March there was some movement of birds from flock to flock and some new birds appeared in flocks where there had been little change all winter. Banders in the Northeast have frequently recorded this early-spring movement with new birds appearing at feeding stations (e. g.), Butts, 1931; Bowdish, 1938). In the present case it was definitely known that part of this

movement was a local shifting of the banded population and part was due to appearance of new birds of unknown origin, or disappearance of banded birds. The break-up of the flock was a gradual process. In one flock which was followed from day to day, pairs or single birds separated out a few at a time until only one or two pairs remained to establish territory and nest on the winter feeding range. In the case of a flock occupying the center of the village, the area was evacuated completely by chickadees thus leaving no nesting pairs. This is undoubtedly what happens in city parks and other places where chickadees occur in winter but do not nest. Some of the birds were followed or later located at nearby points but many could not be found, apparently having moved a greater distance than could be covered in this study. Dispersal was in all directions, but there was a definite tendency to move up the valleys and hills; in winter, birds were concentrated in the vicinity of the village located in the valley and many of the birds moved into the hills to nest.

Despite a close watch on behavior during the pairing period, no clear-cut courtship ritual was observed. In some cases two birds would be seen in flock formation with others showing no particular interest in each other; then several days later would be noted definitely paired and traveling together. In other cases banded single birds were known to separate from the flock and were observed moving about alone; then several days later these birds would be found paired with an unbanded bird. The first unmistakable pair was observed on April 11; the last flock comprising four birds on April 27. After the latter date only pairs or single birds were seen until the appearance of the first young. A total of nineteen pairs involving banded birds was located during the spring. The territories of fifteen of these pairs are shown in Text–figure 1. The case histories of the two best-known pairs are given below. The male of pair no. 1 was present all winter but the female did not appear in the same flock with the male until March 15; hence this pair could not have been mated over winter. Both male and female of pair no. 2 were members of the same winter flock but there was no conclusive indication of their being mated until about April 25.

Pair No. 1 (A-RG and A-BIR)

April 11, 10.45 a.m.—Female, A-BIR, feeding in close company with male A-YR (not her subsequent mate). Female observed to flutter wings lightly when male came near; he, however, made no response to this behavior. 12.15 to 1.00 p.m.—Two above birds now traveling in flock of five birds which includes male A-RG, with male A-RY and female A-YB which subsequently formed pair no. 2. All

five birds fed and moved together in typical flock behavior with no indications of possible pairs. However, male A-RG twice observed chasing male A-RY.

April 12–13.—Snowstorm; flock of eleven birds visiting feeding station intermittently all day including subsequent pairs nos. 1 and 2. Winter behavior entirely.

April 13–19.—Birds visiting feeding station reduced again to five birds noted together April 11. Birds visit station together or singly; no evidence of definite pairing.

April 20–23.—Second snowstorm; eight birds now in flock exhibiting only winter behavior.

April 27.—A-RG and A-BIR noted separated from flock and going to roost in adjacent spruce trees, first evidence of pairing; previous to roosting the birds kept close together and uttered only the low conversational *seep* call. The roosting place was not the same as used by the flock in winter.

May 3.—Pair no. 1 appeared at feeding station while pair no. 2 was there; much *phoebe*-ing and chasing of each other followed with all four birds engaged in the fight. At this time it was clear that pairs were definitely formed and paired birds antagonistic toward others. Also territory establishment was beginning.

May 4.—Pair no. 1 observed going to roost in same place as on April 27.

May 6.—Pair no. 1 observed excavating a cavity about 300 yards from above roost.

Pair No. 2 (A-RY and A-YB)

April 11.—Male A-RY in a flock of five as mentioned above. At 10.40, male also noted alone flying back and forth in the tree tops giving loud *phoebe*-songs.

April 16.—Male noted alone, alternately feeding and calling *phoebe* loudly.

April 24.—Male appeared in tree with pair no. 13 (G-Gr and G-BR), two birds which spent the winter on another winter range and were already paired at this time. Much *phoebe*-ing and chasing followed. Both members of pair no. 13 chased male A-RY until he finally withdrew. This was not a territorial squabble since pair no. 13 later moved out of the region.

April 25.—Male noted with female A-YB, first time two definitely noted together.

April 28.—A-RY and A-YB appear at feeding station together, apparently mated. Birds keep close company and continually call to each other with low *seep* notes.

April 29.—Pair excavating a cavity.

May 3.—Have squabble with pair no. 1 at feeding station as described above.

May 6.—Pair abandoned first attempt at excavation and have nearly completed a second cavity. The territory adjoins that of pair no. 1.

May 11.—Pair at feeding station; female begging and male feeding her; first time this behavior noted in this pair.

Observation on formation of other pairs did not reveal anything very different from the above. If there is a definite ceremony necessary to "weld the sexual bond" as seems to be the case in many species, it is inconspicuous or I have failed to see or recognize it. Definite courtship displays have been described for some Paridae (the Blue Tit, Great Tit, Marsh Tit,—Witherby et al., 1938) involving display of conspicuous markings or 'nuptial flights'. I have found no reference to a courtship display in either the American or the European

atricapillus, although the black-and-white head pattern would seem to have possibilities in this direction. Whether or not there are definite courtship displays, it seems likely from the evidence at hand that pairs form not as a result of a brief conspicuous ceremony but come together gradually as Lack (1940) suggests may be the case in many species, particularly those which pair from flocks. Thus, in the above case histories, the female of pair no. 1 seemed to be pairing with male A-YR on April 11, yet she eventually paired with male A-RG although A-YR remained unmated in the vicinity until April 28, after which he disappeared. Also, birds would be seen alternately scattered and in compact flocks in the same day or on successive days. The two snowstorms may well have interrupted pairing. All this would point to the gradual formation of the pairs.

The problem of pair-formation in the chickadee is made more difficult not only because territory is not involved but also because the sexes are alike in plumage. Chickadees quickly learn to recognize one another as individuals as is shown by the development of a definite dominance order (or 'peck order') in the winter flocks, but this does not necessarily mean that the birds are capable of discriminating sex on basis of appearance alone (Lack, 1940). Consequently, we would expect behavior or voice to be important in sexual recognition and mating. Increasing restlessness and increasing use of the *phoebe*-song are the two most noticeable changes in behavior preceding pairing. Birds were often noted flying back and forth in the treetops and males were several times observed to engage in vocal duels while flocks were still largely intact. Both sexes may utter the *phoebe*-song but the male gives it more frequently and generally much louder. In this region the three-note version was heard about as frequently as the two-note version. Both versions may be given by the same individual and the songs seem to serve the same purpose. In the spring the loud *phoebe*-song given by the male apparently functions to intimidate other males and to attract the females, as indicated by behavior of A-RY noted above. Later, the *phoebe*-song functions in territory defense; at other seasons it does not seem to have a definite function, unless possibly it is used to establish dominance in flocks during late summer when the note is frequently given by young birds. Thus, the same note may serve different purposes or evoke different responses depending on the season and physiological state of the bird.

Dominance undoubtedly plays some rôle in mating. In the winter flocks, males were generally dominant over females, that is, females withdrew or were driven away when they came in close contact (as at a feeding station) with males. There were, however, cases where

females were dominant over certain males. This winter behavior is probably to be classed as social dominance, which, as Noble (1938) has pointed out, is to be distinguished from sexual dominance. In pairs 1 and 2 and in all other pairs where the winter-dominance relations were known, the male was dominant over the female when the two were in the winter flock. However, after pairs had formed or separated out of the flock, I did not observe the male of the pair exert dominance over his mate (except on one occasion when a newly formed pair visited the feeding station). There was no 'pouncing' by the male as Nice (1937) describes as frequent in the Song Sparrow prior to egg laying.

Dominance may also play a part in the relation between males. The two males of pairs 1 and 2 were respectively the top two birds in the 'peck-order' of their winter flock and these two were the only two males which remained to establish territory on the winter range. Male A-GR was about no. 3 in the social order and he nested nearby (see pair no. 3, Text-figure 1). In this case the most dominant males were the most sedentary; or perhaps they were dominant because they were sedentary and had held territory there the previous year. Whether this correlation is significant or simply coincidental, of course, can only be determined through further study of rôle of dominance.

The feeding of the female by the male, called 'courtship feeding' by Lack (1940a), is apparently not part of the courtship in chickadees. True, the male regularly feeds the female during incubation and sometimes during egg laying or nest construction, but with one exception I did not observe this behavior in newly paired birds. Usually from a week to two weeks elapsed between the first observation of definite pairs to the first observation of begging by the female and feeding by the male. In the case history of pair no. 2 above, the birds were paired at least fourteen days and had excavated two cavities before the begging-feeding behavior started. The first pair was observed April 11, while the first observation of begging by a female was May 9.

Whether or not copulation takes place immediately after formation of the pair or is delayed until the nest is under way was not determined, although the later would seem to be the case. Copulation was observed only once (in pair no. 15) curiously enough at a time when the female had already started incubating eggs. During the act the female fluttered her wings and uttered a high-pitched twitter.

Noble and Lehrman (1939) found that in the Laughing Gull courtship ritual was repeated in abbreviated form during ceremonies at the nest; hence it might be possible to obtain clues on courtship

behavior from the more easily observed nesting behavior. When the male approaches the nest during incubation he regularly utters the *phoebe*-song softly and female may answer with a soft twitter. When the sexes meet at the nest both birds often flutter their wings and give high-pitched twitters.

The importance of the loud *phoebe*-note of the male and perhaps also wing fluttering and twittering by the female is indicated by the behavior of birds which had lost their mates. This happened several times during the season. When a female disappears either temporarily or permanently the male calls loudly using both *chickadee-* and *phoebe*-notes, particularly the latter. The most interesting case of loss of mates and remating was as follows:

Pair no. 5 was first observed mated on April 11 and seen again on April 15. Neither was seen again until May 15 when female, R-RB, was seen begging from an unbanded male (thus making pair no. 16) in an adjacent area where the nest was subsequently found (Text-figure 1). Her former mate was not found and had presumably perished. In the meantime, pair no. 6 were excavating a cavity on an adjacent territory (see Text-figure 1). About the middle of May the female of pair no. 6 disappeared. Between May 20 and June 10 the male remained on the territory, was observed to defend it against male of pair no. 8 and spent much time cruising the territory and giving loud *phoebes* at intervals. On June 10, still not having attracted a new mate, he apparently abandoned his territory since he was seen moving in the direction of the territory of pair no. 16. In the meantime the male of pair no. 16 had disappeared on June 12 and female was feeding the young alone on June 15. On June 17, the male R-BY (formerly of pair no. 6) appeared at the nest and was helping the female feed the young. The female was observed to flutter her wings, utter a high rolling twitter, and to hop about in front of male as if begging copulation; the male, however, appeared disinterested and even hopped away when female came too close. Later the performance was repeated; in the meantime, the female continued to feed the young and the male remained near. On June 18, the young left the nest and both adults fed young; however, the male fed less frequently, showed interest in cavities and *phoebed* a great deal. On July 5, male was seen alone *phoebe*-ing and investigating cavities. Finally, the pair returned to the same cavity, laid a new set and raised another brood. This move was a complete surprise so that I did not discover the new set until they were hatched. This pair (no. 17) succeeded in raising the brood and were still together in September. Thus the female, R-RB, had three mates and raised two broods (the only case of a second brood recorded in this study) and the male, R-BY, had two mates and raised one brood.

There were only two other known cases of disappearance of mates in fifteen pairs studied most closely. In one case (pair no. 2) the female disappeared shortly after egg laying. The male remained on the territory a week, spent much time *phoebe*-ing and was observed to have a territorial boundary dispute with male of pair no. 1. He then disappeared, perhaps moving elsewhere in search of a mate. In

the other case the male was accidentally killed in experimental work after young had hatched. The female continued to feed young and care for brood successfully and did not take a new mate so far as was known. No cases of polygamy were encountered in this study.

Behavior of newly paired birds.—After the pair is formed (or separated from the flock) there follows a short period before active nesting or establishment of territory takes place. For convenience, this period will be called the 'pre-nesting period'. The length of the pre-nesting period apparently depends on the lateness of the season and on the weather. It was longest in the case of birds which paired early. For instance, in pair no. 6, fourteen days elapsed between the first observation of pairing (April 15) and the beginning of cavity digging; pair no. 2, which were apparently not definitely mated until April 25, began digging a cavity five days later. The behavior of six pairs was observed closely during the pre-nesting period with a total of ten hours being spent following the birds about.

During the pre-nesting period the pair may remain in the area where they were first observed paired; this area may or may not be within the winter range of one or both birds. However, in at least two cases (pairs no. 4 and 9), the mated birds moved slowly across country for a mile or so before settling down to nest. In one case the birds were actually followed during this wandering movement. Pair no. 13 disappeared from the place first observed perhaps moving completely out of the study area. In other cases pairs were not discovered until after the beginning of nesting, so that it was not known whether or not pairing occurred on the future nesting territory.

In all cases the mates remain very closely associated throughout the day. The daily activities consist of feeding, resting, preening, and sometimes half-hearted examination of possible nesting sites. The two birds generally move leisurely and keep contact with each other through the use of the soft *seep* conversational note, the same note continually given by birds when in flocks. As long as the mates remain together (within five to forty feet) and no enemy appears, there is little other vocal activity; hence pairs are hard to locate unless one's ear is tuned to pick up the soft *seep* calls. If birds stray apart they may employ the regular loud *chickadee* call note to aid in locating each other. If a winged enemy appears, the warning note, a high-pitched *see-see* is given and birds 'freeze', the same behavior and response frequently observed during the flocking period. As previously stated, the female was not observed to beg during the pre-nesting period. In fact, there is nothing in the behavior of the pair to indicate which is male and which female. Neither sex seems to be the leader during

feeding excursions since first one bird then the other would be observed moving ahead. All this behavior is similar to that of non-breeding flocks; in fact, a pair during the pre-nesting period act very much like a flock of two, except for one important thing: the pair in contrast with the flock isolates itself and is antagonistic to other members of the species. If another chickadee or pair is encountered immediate antagonism develops. Both birds call excitedly with the *chickadee* note, various sputtering variations of it, and the *phoebe*-song (particularly by the male). If the intruders come close a mélée follows with birds chasing each other about, or actual fighting may take place. Such mélées were observed several times during latter part of April. Both birds of the pair take part in the protests. Sometimes two pairs would be involved. In another case a pair encountered a single bird and both members of the pair were seen to chase the single bird. In still another case, five or six birds, perhaps three pairs, were involved in a mélée although it was difficult to determine just what was going on. Generally, after several minutes of loud calling, chasing, and flying about the pairs drift apart and go on their way. In several cases the fighting was clearly a defense of mates and not territory since the birds involved later established territory elsewhere and the area where the fighting took place was not a part of these territories. To follow the terminology of Noble (1939), this fighting might be interpreted as defense of a 'sexual territory' as contrasted with a later-established 'nesting territory'.

TERRITORY

Establishment.—As has been previously indicated, the territory in the chickadee is principally a nesting territory which may or may not coincide with the area where mating takes place. Also, as just described, paired birds may cruise about for several days before establishing a nesting territory on which they remain fixed for the nesting period. Several pairs established territory immediately on the wintering range occupied by both birds. However, in most cases the territory and the winter range did not coincide. Establishment of territory seems to begin about the time of the start of nest construction; it is quite probable that the finding of a suitable nesting site is a determining factor in territory establishment.

Defense.—As I interpret my observations, fighting for the mate (or 'sexual territory') gradually changes to fighting for territory ('nest territory'). Thus, when a pair encounters other chickadees during random movements of the pre-nesting period the birds become antagonistic to other chickadees but 'defend' only a small area around

themselves. When territory is established on the other hand, an area of considerable size is defended. That defense of territory is definitely separate from defense of mate, is shown by the fact that the male will drive another male out of the territory even though his mate is not present on the occasion (observed three times), or the male may even defend the territory vigorously against another male even when his mate has been lost (observed twice).

The male assumes the leading rôle in defense of the territory although the female may join him in the defense. I did not observe the female defending the territory alone. The defense procedure does not seem to be as elaborate in the chickadee as Nice (1937) describes for the Song Sparrow. In the Song Sparrow there are five parts to the defense behavior; from observations on the chickadee I would distinguish at most three parts, as follows. (1) The challenge: When a territory is invaded the male challenges the invader with loud *chickadee* calls and especially loud *phoebes.* The invader may answer the challenge with similar notes resulting in a 'vocal duel' or he may retire immediately. (2) The chase: If the invader stands his ground a chase follows with one or both birds chasing the other. Preceding the actual chase birds may fly back and forth near each other with loud *phoebe*-songs. (3) The fight: In one case an actual fight was observed in which the birds tangled in mid-air and fell to the ground together. This occurred on the boundary of two established territories and after the fight the males retired to their respective areas. In general, the defender takes the initiative in calling and chasing, and the invader either retires or dodges the attacks. No wing fluttering or 'puffing up' was observed although during the challenge the male stands very straight and, I believe, may raise the feathers on the head bringing the black-and-white pattern into prominence. According to Tinbergen (1937) territorial quarrels of Great Tits mostly take the form of threats involving display of color marking and other behavior rather than, or in addition to, the use of vocal powers.

The chickadee does not regularly proclaim or announce ownership of its territory, which is interesting in view of the fact that so many passerines spend much time announcing by song from exposed perches. Once settled on a territory the male (as well as female) sings very little, if at all, so long as he is successfully mated and is not challenged by another bird. The male rarely sings regularly from an exposed perch. A nesting pair of chickadees is usually very silent and often hard to locate after nesting is under way as is also indicated by frequent references in the literature to the "disappearance" or "shyness" of chickadees during the nesting season. Consequently, the singing-male

method of censusing cannot be used in determining the population of nesting chickadees. A chickadee which is doing a lot of singing is usually an individual looking for a mate or one having territorial trouble with a neighbor or intruder.

The chickadee does not regularly defend its territory against other species as does the Song Sparrow (Nice, 1937). Only once was a chickadee observed to make a hostile move toward another species other than a predator; in this case a male chased away a transient Brown Creeper that happened to alight on the nest tree during nest excavation. Often pairs of chickadees are accompanied in their movements over the territory by warblers and other transients, the same association which frequently occurs in the fall flocks.

The territory seems to be defended until the young leave the nest, although defense was observed most frequently during the early part of the cycle while territories were being formed and many birds were still unsettled. Defense was observed only twice after hatching of the young. On one occasion the male challenged and chased out a lone unbanded bird while on the way to feeding the young. In the other case, the young had just left the nest; the adults were scolding me when a lone unbanded adult appeared, probably attracted by the scolding. The parents immediately stopped scolding and began chasing the intruder; first the male, then the female chased the bird until it retired.

Soon after the young leave the nest, territory defense apparently stops or becomes very weak; even before this, flocks of young birds may be tolerated. One male which was feeding young in the nest paid no attention to a small flock of juvenile chickadees which entered the territory from an adjoining area. One of these juveniles was observed to beg from the male, but he did not feed it.

Most cases of territory defense were observed between rival males of adjacent territories as indicated in Text-figure 1. As can be seen from this figure the density of population was not great and except at certain points the territories were not crowded together. With a higher population more territorial fighting might be expected.

Size of territory.—Text-figure 1 shows the territories of all the pairs nesting on the Preserve and also of a few pairs in adjacent areas which were watched closely. The heavy dotted lines outline the maximum area known to be patrolled and defended by birds during the early part of the nesting cycle of the first nesting attempt. The numbers indicate the pair which occupied the territory. The solid lines between territories indicate points where boundary disputes between rival males were actually observed. In the case of pairs nos. 15 and

8 territorial defense by rival males was observed three times at the same place. Each time the behavior of the two birds was very similar, the same trees, almost the same limbs being used during vocal challenging and chasing. Finally, both birds would retire to their respective sides continuing to challenge each other. On June 1, the male of pair no. 8 had a border dispute with the male of pair no. 6 at 9.45 a. m., then at 10.00 a. m. moved over to the other side of his territory and had a fight with male of pair no. 15, his other neighbor. The repeated occurrence of disputes at the same point suggests that where pairs are close together and territories crowded, the boundaries may be very sharp, almost as if there were an actual line. On the other hand, where there is no pressure from neighbors the boundaries seem to be much less definite, as for instance the south boundaries of the territories of pairs no. 8 and 15. Territory boundaries are indicated in Text-figure 1 by dotted lines in order not to give the false impression of absolute sharpness of limits. The longer the observation the more it became apparent that borders fluctuated from time to time, especially as the nesting period progressed. It was only at points of contact that boundaries seemed sharply established.

With the aid of a planimeter the size of the territories as drawn in Text-figure 1 was calculated. Territories varied from 8.4 acres (3.4 hectares) to 17.1 acres (7 hectares) with an average of 13.2 acres (5.3 hectares). There would probably be less variation in size of territory if the volume of the habitat rather than the area could be determined since the larger territories (pairs nos. 1, 2, 11) contained considerable open or sparsely wooded country. It is interesting to note that the average size of the winter-flock range was 20 to 25 acres, so that the territory of a pair was about half that covered by the average flock during the winter fixation period. In spring or fall, of course, individuals, pairs, or flocks may range more widely.

As previously mentioned, Text-figure 1 represents size and shape of territories at beginning of the nesting cycle. If a close study of three or four of the pairs can be judged as representative, the size of the territory decreases as the nesting period progresses. Thus, during building, egg laying, and incubation birds avoid the vicinity of the nest except when engaged in attentive duties and spend much time ranging over the territory feeding or resting. On the other hand, when the young hatch the parents tend to gather food near the nest. This tendency increases progressively until by the time young are ready to leave, the parents are flying only a short distance for food, as Butts (1931) also noted. True, they may still occasionally visit the other part of the territory, but much less frequently and hence would

have little occasion to defend it. Pair no. 15, which was observed frequently, covered only about half the area while feeding the young that they did during incubation. This would seem to support the contention that territory establishment is not for the purpose of conserving a food supply since not nearly so large an area as was originally staked out is needed when the demand for food is greatest. Therefore, the function of the nesting territory in the chickadee must be simply to protect the pair from the disturbing influences of other chickadees during the period of nesting.

Habitat.—The chickadee territories very often included two distinct habitats. In Text-figure 1, the area under study is divided into three broad habitat types represented by three stages in vegetative succession: (1) abandoned fields covered with herbs and shrubs representing early seral stages; (2) young forests or 'second growths' of cherry, birch, aspen, willow, ash and maple or combinations thereof representing intermediate seral stages; and (3) mature forests of elm, ash, maple, beech-maple, beech-hemlock, etc., representing advanced seral stages. Young conifer plantations (1a) which represent an artificial early seral stage as well as the numerous hedgerows (2a) which ecologically are probably to be included under (2), are also indicated. Abandoned fields either naturally or artificially reclaimed were not occupied appreciably during the nesting season so that territories were established in types 2 and 3. Furthermore, both types were often included in a given territory (Text-figure 1) since the nest was often located in a comparatively open situation, such as a young forest, hedgerow, or field border, and the feeding-resting activities were largely carried on in deeper woods. Thus, to use the terminology of European bird ecologists, the nesting biotope often differed from the feeding-resting biotope as is illustrated by territories 1, 7, 10, 15, and 16. Mayr (1928) described the same thing for the European *atricapillus* or Willow Tit. Territory 10 is especially interesting. The nest was located in a cherry stub out along a hedgerow with open fields or pine plantations on all sides. The birds when not engaged in nest duties spent all their time in the woods and were frequently observed flying back and forth along the hedgerow from nest to woods. Such a double-habitat territory would seem to result from the type of nest tree needed. The chickadee is unable to dig a cavity except in very soft or rotten wood. The most suitable soft-wood trees such as birch and pin cherry occur as living trees in the early seral stages but are short-lived and persist in the intermediate seral stages as decayed stubs. By the time the mature forest develops, all are gone and the dead timber is mostly harder wood less suitable for

excavation. Where woodpecker holes are used (as by pair no. 4) or bird boxes this nest-habitat requirement might not be a limiting factor.

Population.—Ten pairs of chickadees established territory within the approximate boundaries of the Huyck Preserve at the beginning of the season. Since the Preserve contains 476 acres this represents one pair to 47.6 acres, or, excluding the 103 acres of water, one pair to 37.3 acres (15.1 hectares). If, however, we exclude the 153 acres of field habitat and conifer plantation which were not occupied by nesting birds, we get one pair to 22 acres (9 hectares) of chickadee habitat. Butts (1931) found two pairs nesting on the 80-acre Fuertes Sanctuary in two successive years. The total area of the ten territories on the Preserve is 121 acres, leaving 99 acres of chickadee habitat unoccupied. Since the average size of all territories was 13 acres it might be concluded that the area could have supported seven more pairs or a total of 17 pairs. However, it seems probable that this theoretical density would never be reached, at least not with the arrangement and size of territories as existing in 1940. As can be seen from Text-figure 1 there is room for only three or four more territories which would be likely to include the proper nesting and feeding biotopes. There seems to be room for territories on either side of no. 11, between nos. 9 and 17 and perhaps at one or two other places. These areas have suitable nesting stubs.

The total chickadee population in winter was approximately 50 to 60 birds as compared with the summer population of 20 and the theoretical maximum of 34 birds. Hence it appears that the area is capable of supporting more chickadees in winter than in summer. This suggests that the territorial habit together with the nesting requirements are important factors in regulating breeding-population density.

DISCUSSION

As has been indicated, the territorial behavior of the chickadee differs from that of many passerines in two respects: (1) territory is established after, rather than before pairing, and (2) the birds do not make themselves conspicuous on it. Thus, neither Tinbergen's (1936) definition of territory (i. e., "an area which is defended by a fighting bird shortly before and during the formation of the sexual bond") nor Mayr's (1935) definition ("an area occupied by a male of a species which it defends against intrusions of other males of the same species and in which it makes itself conspicuous") is strictly applicable to the chickadee. Yet the chickadee is certainly territorial since

the pair restrict themselves to and defend an area during a part of the breeding season. The more the territorial behavior of different species is studied the more evident it becomes that the term 'territory' should not be defined too closely if the concept is to be useful in the study of birds or vertebrates generally. Rather, different kinds of territory should be recognized as Noble (1939) has pointed out. The chickadee may be said to hold a 'nesting territory' but apparently not a 'mating territory' or at least the two may not be the same.

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