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AN ANALYSIS OF FLOCK ORGANIZATION IN
BLACK-CAPPED CHICKADEES

by

John Ivan Mosher

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Zoology

Approved:

Major Professor	Committee Member
Committee Member	Committee Member
Committee Member	Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

1972

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John Ivan Mosher

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ABSTRACT

An Analysis of Flock Organization in Black-capped Chickadees

by

John L. Mosher, Doctor of Philosophy

Utah State University, 1972

Major Professor. Dr. Keith K. Dixon
Department: Zoology

An analysis was made of individual behavior and flock organization among 33 color-banded Black-capped Chickadees (Parus atricapillus) on a woodland tract in wester New York State, from December 1967 to June 1970. Also, three of these flocks were confined at various periods for an average aviary tenure of 26 days. From these observations I concluded that the hierarchy and interindividual relationship of a flock remain as observed in the field; testosterone propionate causes an increase in injected subordinate bird's activity; but did not effect a change in its rank.

From the observations in the aviary, it was found that subtle differences in male and female bibs and caps facilitated sexing of the chickadees. All 9 resident flocks of adults usually consisted of 4 birds (9 of 11 flocks) and had a 1:1 sex ratio, whereas first-year and itinerant flocks were more likely to have an uneven sex ratio, indicating that these flocks were not made up entirely of pairs. All flock members observed through the breeding season

mated with other members of their flock. Nest sites were heavily concentrated in a section of dead trees near the border of the coniferous sector. Six nest boxes placed in the coniferous woods were not used, though fifty percent of the breeding territories on the study area included coniferous woods, and the birds with the longest tenure in the area used the coniferous woods as part of their winter flocking range and breeding territories.

Establishment of feeders affected patterns of flock size and behavior. Also the alpha male's mate took precedence over other flock members at a restricted food source. From other observations of alpha males, it was noted that in one instance in three winters one resident flock disbanded, with its alpha male taking a beta position in its new association, and the beta male becoming the alpha of another flock. Also, it was discovered that the removal of the alpha male from flocks of free-living and confined chickadees for a two day period did not result in disorganization of the flock.

All resident flocks and 2 flocks of first-year birds exhibited a linear hierarchy. Further observation of first-year flocks confirmed that there was no special relationship or pair bond among the male and female members; however, both males and females were present in these flocks and mated with flock members. These flocks of first-year birds also seemed to function as a reservoir for replacing lost members of resident flocks, the formation of which was deferred by the adults until the young dispersed. The independent young formed large bands and ranged widely.

From observations in the aviary it was found that there was no change in hierarchy from that observed for the flock in the wild. Also in the aviary, the subordinate male bird received three injections of testosterone propionate. No apparent elevation in his social position was observe. However, a statistically significant ($P = 0.01$) increase in activity among members of one of the flocks was recorded. Finally, caching of surplus food was observed both in the wild and in captivity.

Contrast in social relationships of adult and first-year birds prior to onset of breeding is more pronounced than heretofore recognized. First-year birds apparently are not paired, and tend to travel more widely in flocks that may be larger than those of resident flocks.

Learning appears to be the most important response in the organization of the resident flocks.

(110 pages)

INTRODUCTION

Recent studies of the social behavior of birds have concerned themselves mainly with two problems: the mechanisms of integration of the organized social unit, and the effects of the social environment on activity, fecundity, and survival (Emlen, 1952; Crook, 1961, 1965). The means by which the first of these, flock integration, is achieved continues to baffle investigators. In looking for answers one is impressed by three attributes of flocks: (1) cohesiveness; (2) individual recognition and the dominance hierarchy; and (3) permanent pairing.

Hinde's (1952) observation on cohesiveness indicated that visual and auditory communication are influential in integrating a flock of Great Tits (Parus major). He stated that

> A typical integrated movement takes place as follows. The birds are feeding on the ground when one of them flies up into a low bush and starts calling "twink, twink." As he calls he hops higher and higher in the bush. His calling has no apparent effect on some of the birds, but others stop feeding and also hop up into the bushes, twinking. After a short while (say 1/4 minute), one bird flies off, and one or two others follow him. These leading individuals fly from bush to bush calling between flights. The remaining birds gradually stop feeding and hop up, calling, one by one until all have moved off. . . . there are no fixed leaders, and successive movements may be initiated by different individuals. (Hinde, 1952, p. 9)

Crook (1961, 126) citing Moynihan and Hall, stated that ". . . there are indications that birds' gregariousness is really more than an aspect of other 'drives'." The birds appear to do more than sleep, feed and preen together. (Moynihan and Hall say. "They certainly look as if they just want to be together.") Activity cycles, such as feeding, drinking, sleeping, hopping about, washing and preening, are useful for revealing certain features of flocking behavior (Crook, 1961). He stated (page 128) that "There is an interrelation between cycles of these activities in individuals that produce a group cycle."

From these statements it seems that the tendency of the bird to follow another (following reaction) and the copying of the behavior of one individual by another (social facilitation) are two powerful factors promoting cohesiveness in bird flocks.

Eibl-Eibesfeldt (1970, 351-352), commented in the relationship of rank to group integration in his statement that "The dominant animal may ensure [sic] the cohesion of the group by breaking up fights; it may assume the function of leadership in certain respects, such as determining the time for moving on and by giving the direction during migrations." If indeed rank is a factor in group cohesiveness, then all the factors which influence the rank of an individual would consequently be involved in the mechanisms of integration. The most influential factors vary with the species. For example, Dixon (1965) found seniority on the area was a factor influencing social position in the Mountain Chickadee. The alpha bird of a flock was the oldest resident of the area. Dixon (1965, 293) stated, "The data indicated that a linear ranking was found wherever the birds traveled, and that the relations among flock members were of a peck-right type." His conclusions were confirmed by Minock (1971).

In the genus *Parus*, winter flock hierarchies based upon individual recognition have been observed by Colquhoun (1942) in *Parus oaeruleus*; Hamerstrom (1942), Odum (1942) and Hartzler (1970), in *P. atricapillus*; Brian (1949) in *P. Major*; Dixon (1963) in P. *carolinensis*: Dixon in P. *gambeli*.

Allee (1951) commented on interindividual recognition in flocks of domestic chickens (*Gallus gallus*) as being necessary for the maintenance of the flock hierarchy. The flock hierarchy in chickens seems to break down when the flock becomes too large for individuals to recognize each other (such as in mate recognition) but in order to sustain a flock hierarchy each individual must recognize every other and remember its social position relative to his.

In flocks of chickadees subordinate individuals respond not only to the dominant male but also may be subordinate to his mate. M. E. Minock (pers. comm.) has observed the alpha male in a winter flock of Mountain Chickadees defer his feeding activity at a food sources while his mate of the previous breeding season was feeding there. I have also observed this in the Black-capped Chickadee. Lorenz (1938) concluded from his studies of the Jackdaw (*Corvus monedula*) that a female's rank is influenced by the rank of her mate. Dixon (1963, 246) observed in *Parus carolinensis* that the alpha bird's mate had precedence at a restricted food source in alpha's presence. "However, in the absence of their mates such females did not always hold precedence over subordinate males." Observations of the special treatment accorded his mate of the past breeding season by the alpha, but not extended to other flock members, seem to indicate mate recognition. The special recognition of the alpha's mate by other members of the flock is illustrated by Dixon's (1965) observation of the beta male in a flock of Mountain Chickadees, becoming bold and supplanting alpha's mate in the alpha's absence. Dixon (1965, 293) stated (in referring to the beta male) "This pugnacious attitude was dropped when the alpha male reappeared following his release from temporary captivity." Clearly this indicates some influence of the male's rank on the status of his mate, as well as interindividual recognition.

Factors which have been recognized as having some influence on the social ranking of individuals include sex, learning ability, age, size, decline in vigor, sexual dimorphic aspects of plumage, mating status-with or without offspring (Marler and Hamilton, 1966; Eibl-Eibesfeldt, 1970), and tendency to engage in such overt activities as fighting, bluffing or passive submission (Collias, 1944).

Various species of the genus Parus are well noted for the continuity of the pair bond. Wallace (1941, 52) mentions ". . . the tendency of certain individuals of wintering and migrating flocks to stick together not only through one season but more or less permanently." This observation which he made on the Black-capped Chickadee suggests that mates could recognize each other. As a result they could remain together and form the basis for flock organization. Such flocks composed of pairs therefore would have a 1:1 sex ratio. However, in the same species, Hamerstrom (1942, 33) stated, "No individual Chickadee appeared to show a preference for feeding with any other individual, and no sign of friendships or the formation of cliques was noticed." These comments imply that birds mated previously do not show recognition of each other once the winter flock has assembled. Thus, a deterioration of the pair bond would occur over the winter. If no strong, lasting pair bond remained after the nesting season one might expect to find that flocks were unisexual or unpredictable regardless of age or past mating status of the individual.

Conditions generally recognized as having an influence on a bird's social rank include learning ability, age, size, sexual dimorphic aspects of plumage, mating status-with or without offspring, vigor prior residence on an area and sex

The general dominance of males over females (Marler and Hamilton, 166; Eibl-Eibersfeldt, 1970) leads one to suspect that hormones influence aggressiveness and general activity of an individual, and, thus, its social rank. Collias (1944, 118) stated "The most striking fact of endocrine physiology in relation to aggressive behavior has been the persistent association in the vertebrate series of male hormone with aggressive behavior." The physiological condition of an animal has been illustrated by many to have an effect on both its response to flock mates and their response to it.

Experiments employing androgens conducted on wild and captive birds have produced varying results. Testosterone propionate has been found to affect one species of birds differently from another. Emlen and Lorenz (1942) indicated that testosterone propionate implants caused some free-living male valley quail (Lophortyx californious) to become pugnacious, although it did not affect their position in the peck order of the covey.

In referring to experiments using testosterone cyclopentylpropionate injections in Japanese quail, Selinger and Bermant (1967, 267) stated that "The level of aggressive activity could be manipulated by varying the level of circulating androgen." Crook and Butterfield (1968, 383) stated that "Testosterone administration to low ranking members of a six-bird hierarchy of male Quelea quelea produced no significant changes in measures of their ability to win encounters in individual distance infringement."

Upward social mobility was observed in some domestic chickens after treatment with testosterone propionate (Allee et al., 1955). Guhl (1958) found that chicks of the same species treated with testosterone and oestrogen formed peck rights earlier than those not treated. Testosterone propionate treatment of the subordinate male bird in Japanese quail (Coturnix coturnix japonica) caused a rank change. The subordinate male moved to the alpha position while the former alpha bird dropped to the beta position (J. I. Mosher unpublished). In experimenting with starlings (Sturnus vulgaris), Davis (1963) showed that, contrary to its effect on chickens, testosterone did not result in a change in rank.

Emlen and Lorenz (1942) observed that although testosterone propionate did not affect individual male valley quail's position in the peck order of the covey it did affect mating behavior. They found that mating behavior occurred (in non-breeding season) in 3 males and 2 females treated with implant of testosterone propionate. Prococious sexual behavior in turkey poults was induced by Schein and Hale (1959) when they administered testosterone propionate to them. Phillips and McKinney (1962), found that testosterone propionate given to castrated mallard drakes (Anas platyrhynchos) (25 mg. every third day) resulted in a demonstration of all courtship displays. Castrates without the hormone injections gave only occasional pre-copulatory head-pumps.

Butterfield and Crook (1968) suggested that nest building in weaver birds (Quelea quelea) is under testosterone control. These various experiments employing testosterone do not show a consistent effect on the social rank of birds. However, there seem to be definite effects on the relative aggressiveness and sexual behavior of the treated animals. Guhl (1961, 1241), stated that "No gonadal hormones have been discovered which influence gregariousness (other than sexual and parental bonds)."

For studies on various aspects of behavior described on the preceding pages, the Black-capped Chickadee was chosen. It is an abundant, relatively sedentary non-game bird that forms close-knit flocks in winter and separates into breeding pairs in the spring (Butts, 1931; Odum, 1942; Smith, 1967). Also, it can easily be baited to feeders, caught, banded, and observed in its natural habitat with no apparent disruption of its normal behavior. The Black-capped Chickadee is an arboreal, omnivorous bird. It nests in cavities in soft or dead wood which it usually excavates. It is relatively tame and in general shares similar behavioral characteristics with other members of the species _Parus_. Because of these traits it provides an ideal subject for study of flock organization.

The objectives of this investigation are to answer the following questions concerning the social environment: Is there constancy of flock organization in the wild and in captivity? Is the size of the flock limited? Is ther age segregation among flocks? Is the sex composition of the resident flocks predictable or is it unpredictable? What are the effects on the flock of removal of the alpha individual? What are some of the mechanisms of flock recruitment? What is the effect of testosterone on the subordinate male bird's rank and response to other flock members?

THE STUDY AREA

The study area is located about 4 miles south of Lake Ontario, in the township of Carlton, 1 mile south west of Kent Post Office, Orleans County, New York. The area, situated at about 43^{o} 18' N lat., is characteristized by severe, windy winters. The lowest temperature recorded during the study was 0^{o}F and the highest winds at 25mph. gusting to 35mph. Snow persists in the area from early December until early March, with occasional snowfall in late October and early April. Thaws occur during this interval. The growing season extends from late April to mid-August.

The study plot (Figure 1), some 40 acres on level terrain, consists of an eleven-acre planting of 30 year old conifers, bounded on the west by a small seasonal stream. On the western bank of this stream lies a 29-acre section of typical Lake States (Spurr, 1964) deciduous climax woods.

The trees of the eleven acre coniferous portion are about 50 percent white pine (Pinus strobus), 25 percent red pine (Pinus resinosa), 12 percent Norway spruce (Picea abies), 12 percent tamarack (Larix laricina), and one percent white cedar (Thuja occidentalis). Due to the closeness of the plantings, the forest floor receives quite subdued illumination. Needles, twigs and branches compose the floor litter. An understory is nearly non-existent; however, in some areas a slight break in the canopy permits the intrusion of saplings of maples (Acer saccharum), white ash (Fraxinus americana), hop

Figure 1. Map of the study area located in the township of Carlton, Orleans County, New York. Physical features and vegetation are as marked and are the same for following unlabeled maps.

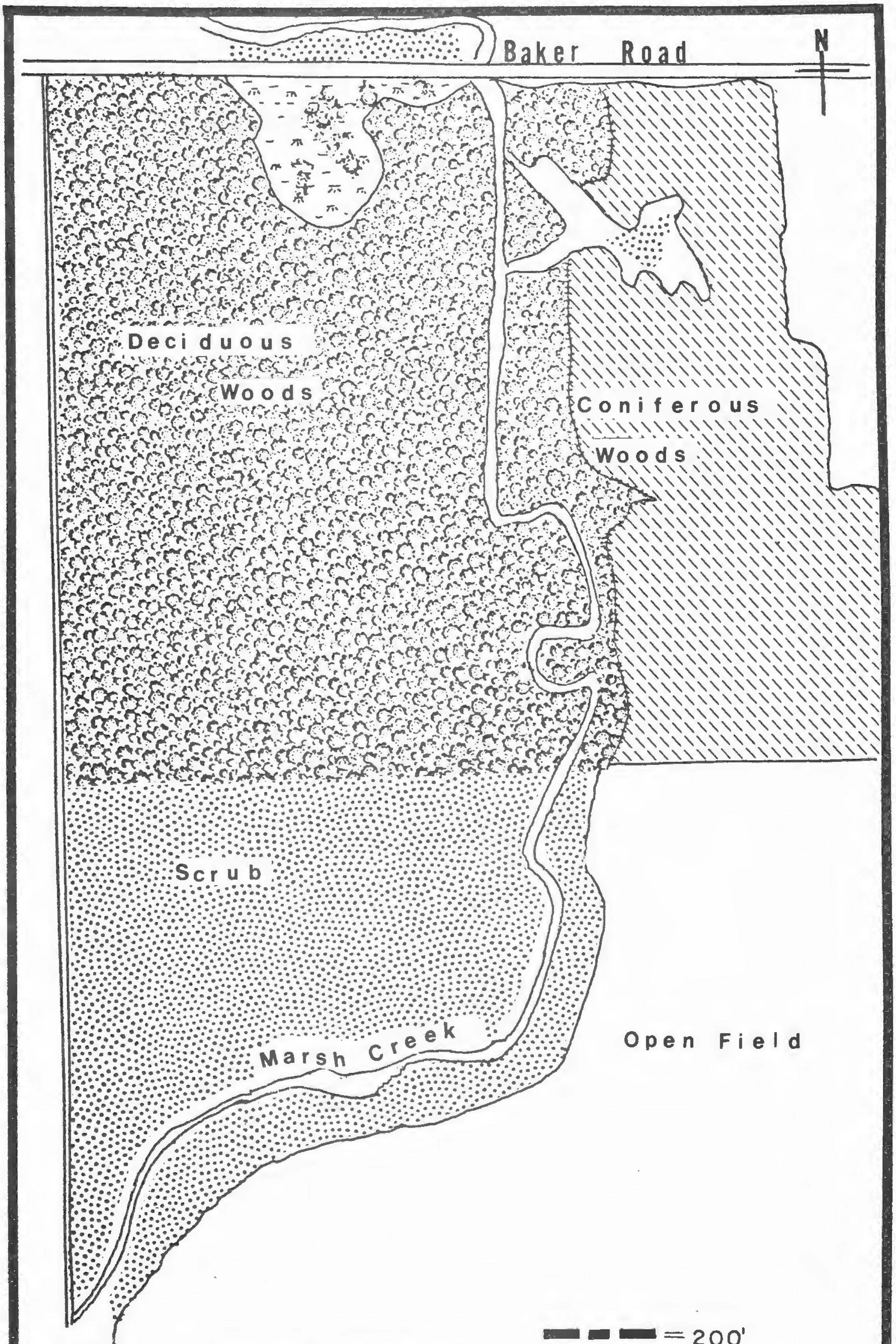

Baker Road
N
Deciduous Woods
Coniferous Woods
Scrub
Marsh Creek
Open Field
= 200'

Fig. 1

hornbeam (Ostrya virginiana), and an abundance of poison ivy (*Rhus toxicodendron*).

The dominant species of the 29- acre deciduous sector are sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*). Other tree species composing the overstory stratum listed in order of abundance are: basswood (*Tilia americana*), American elm (*Ulmus americana*) (represented mainly by the dead remnants of trees infected by the Dutch elm disease), white ash (*Fraxinus americana*), wild black cherry (*Prunus serotina*), tulip tree (*Liriodendron tulipifera*), red oak (*Querous borealis*), black oak (*Q. velutina*), sycamore (*Platanus occidentalis*), and yellow birch (*Betula alleghaniensis*). The understory is composed of seedlings and saplings of the overstory trees, and various woody plants, mainly of the genera *Viburnum*, *Vitis*, *Ostrya*, *Carpinus* and *Benzoin*. Similar woodland extends to the north and south of this plot. Bordering on the south east edge of the deciduous wood is a scrub area. The dominant woody vegetation is staghorn sumac (*Rhus typhina*). Other woody species found in the scrub area and the bordering hedge rows are: quaking aspen (*Populus tremuloides*), pawpaw (*Asimina triloba*), hawthorn (*Crataegus beata*), red and black berry bushes (*Rhubus spp.*), wild black cherry (*Prunus serotina*), choke cherry (*Prunus virginiana*), red maple (*Acer rubrum*). To the southeast and east of the scrub area are fields with a covering of alfalfa (*Medicago sativa*).

Some of the other species of birds frequently observed on the plot were Blue Jay (*Cyanocitta cristata*), Brown Creeper (*Certhia familiaris*), Cardinal (*Richmondena cardinalis*), Downy Woodpecker (*Dendrocopus pubescens*), Hairy Woodpecker (*D. villosus*), Golden-crowned Kinglet (*Regulus satrapa satrapa*), Red-breasted Nuthatch (*Sitta canadensis*), White-breasted Nuthatch (*S. carolinensis*). Some of the "summer resident" birds present during the breeding season were Catbird (*Dumetella carolinensis*), Oven-bird (*Seirus aurocapillus*), Robin (*Turdus migratorius*), Song Sparrow (*Melospiza melodia*), Towhee (*Pipilo erythrophthalmus*), Woodcock (*Philohela minor*), and Yellow Warbler (*Dendroica petechia*).

METHODS

The maps of the study area in western New York State were made from aerial photographs, combined with surface surveys (Figure 1). For accuracy in recording locations of birds and nests, a grid system was set up over the study area. This system was established by using Brunton compasses and running perpendicular north-south and east-west lines, each intersecting to make a 24 yard square area. Each corner of the 24 yard square area had a flag with a number and letter denoting a corresponding coordinate on a mimeographed map. Locations of bird activity then were recorded on the working (mimeographed) map by noting the marking flag closest to the activity.

Play-back tape recordings of the "chickadee dee" call and "phoebe" (feebee) song were used in May, June and July, with varying success, to aid in defining nesting territory boundaries. Details of these territories were entered on the maps.

Analysis of the relative species density was done by the Bitterlick (variable-radius plotless) method (Phillips, 1959).

The Black-capped Chickadees in the study area were trapped or mist-netted and color-banded from December, 1967 to February, 1970. Ages of newly trapped chickadees were determined from late July to mid-November by slitting the scalp to note the amount of skull pneumatization (Miller, 1946;

Nero, 1951). The age of the first year birds was ascertained by new "bright" (i.e., not faded or worn) appearance of the body feathers, wings and wing coverts in June and July and the lack of skull pneumatization. From 25 July to 23 November the skull pneumatization method was used exclusively in age determination.

At the time of capture the birds' rectrices were painted various patterns with Testor's colored airplane cope to facilitate identification at a distance. The traps employed were a modification of the single-cell, swinging drop gate, wire mesh type used by Dixon (1963). Several elevated feeding stations were established and baited with walnut meat to facilitate trapping and observation of flock feeding behavior. In December, 1967, a sunflower seed dispensing feeder was added and in December, 1968 two additional seed-dispensing feeders were added, to aid in determining ranges of various flocks. Climbing spurs and rope were used to investigate nesting sites in higher trees.

Forty-six Black-capped Chickadees were marked during the period December, 1967, to February, 1970. Of this number 26 were determined to be adults and 20 were recorded as immature or first year birds.

Daily observations of the color-marked chickadees were made at the close of the breeding season to ascertain the details of shift from family group to flock organization. At other times of the year approximately 12 hours a week were devoted to observations to determining changes in population and flock interaction. A total of 1,135 hours of field observation was made in this study.

Selected individuals were removed from the flock temporarily to aid in analysing flock structure. In all cases these were the alpha males and the interval did not exceed 2 days. A total of 16 flocks was observed over the period of the study. These flocks, including their identification and the winter they were observed, are listed in Table 1.

In addition to flocks that had been studied in the wild, birds were extensively observed in an aviary, located in an isolated room on the basement floor of Science Building I (Lennon), on the campus of State University of New York College at Brockport, New York. The room in which the aviary is located has proper ventilation but no windows. This room measures 22 X 11 X 10 feet and a portion of this room measuring 4 X 11 X 8 feet is partitioned off for use as an aviary. The partition contains a 2 X 3 feet one-way glass window for undetected visual observations. It also has an access door at one end. The light source is two 40-watt white flourescent tubes 51 inches in length. The photoperiod is controlled by an electric timer. The interior of the aviary is provided with boughs from native trees creating an environment similar to that which the Black-capped Chickadees encountered in their natural habitat. The constant aviary temperature during the study was 67°F. The day length was kept at 9 hours at all times, roughly corresponding to the shortest winter days at that latitude. The food source consisted of seeds, buds, insect larvae and suet.

In the aviary three winter flocks were observed separately for a total of 102 hours. The aviary flocks were first banded and the hierarchy

Table 1. Number of flocks of Black-capped Chickadees observed per winter

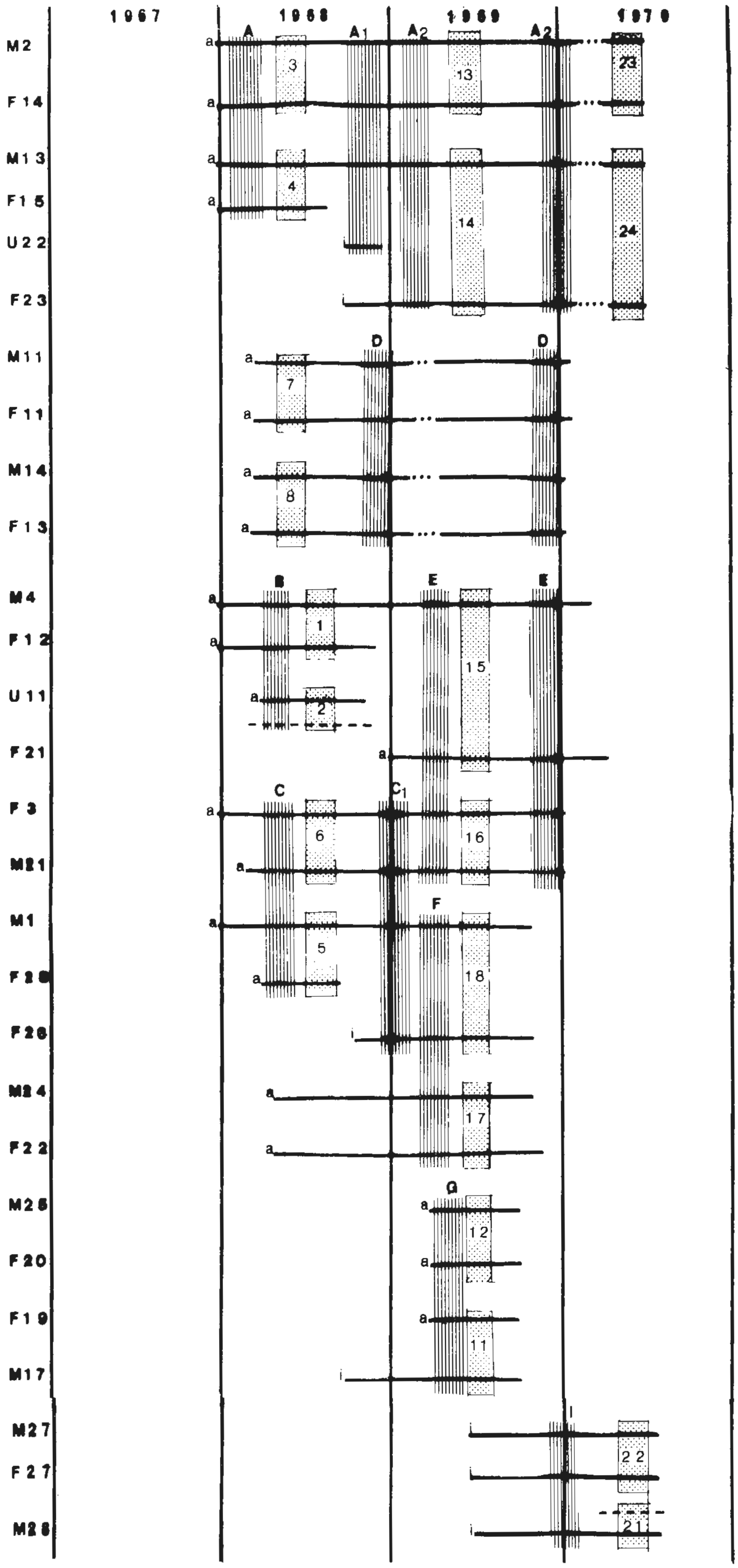
Flock	1967-1968*	1968-1969*	1969-1970*
A1	X		
A2	X		
A3		X	X
B	X		
C1	X	X	
C2		X	
D		X	X
E		X	X
F		X	
G		X	
H			X
I			X
Total	4	7	5

---

*The approximate period of time for each flocking season that these flocks were cohesive units is represented in Figure 2.

X Designates the flock was observed during the winter indicated at the top of the column.

Figure 2. Temporal and social relations of Black-capped Chickadees on the study area. Horizontal bars indicate tenure of marked individuals, dashes that of unmarked birds, rows of dots period of captivity. Rectangles with background of vertical lines enclose the horizontal bars representing members of a given flock during the time interval charted, and rectangles with dotted background denote breeding pairs. Number in those rectangles refer to territories mapped (Figures 6, 7, 8). The letters a and i to the left of certain horizontal bars denote skull-determined ages at the time of initial capture. Capital letters A to I represent flock designations. Subscript numeral denotes change in flock membership. Birds of unknown sex are designated by the prefix U.


1967
1968
1969
1970
M2
F14
M13
F15
U22
F23
M11
F11
M14
F13
M4
F12
U11
F21
F3
M21
M1
F25
F26
M24
F22
M25
F20
F19
M17
M27
F27
M26
A
A1
A2
A2
D
D
B
E
E
C
C1
F
G
I
a
i
3
13
23
4
14
24
7
8
1
15
2
6
16
5
18
17
12
11
22
21

determined in the wild. The hierarchies of the flocks prior to captivity and again during captivity were determined by the following criteria:

(i) supplanting attacks (Hinde, 1952), one individual displacing another either from food or perch;

(ii) chasing of an individual from the vicinity of food;

(iii) withdrawal upon approach of a higher ranking individual;

(iv) waiting by one bird until another has terminated the feeding activity (Dixon, 1965).

In each case the entire flock was trapped and subsequently placed in the indoor aviary. Inclusive dates of captivity are shown in Tables 7, 8 and 9. The total observations for any one flock averaged 22 hours. However, the birds were observed an average of 14 hours before the subordinate male in each flock (A3 and D) was treated with testosterone propionate. Tables 7, 8 and 9 depict flock hierarchies in the wild and before treatment in captivity.

The sex of various members was determined by breeding behavior and the Mosher-Lane method (Appendix I), but remained unknown for some individuals.

Numbers assigned to individuals (Figure 2) were based on the order of original banding and indicate the year of their first appearance (single digits for 1967-68, 10-19 for 1969-70, etc.). Designations for territories in subsequent figures follow the same scheme. Letters denote the chronological order in which parties of birds were recognized as coehesive flocks. Designations with a subscript numeral indicate that a cohesive flock has undergone some change in membership. (For example, flock A1 was the original flock recognized as a cohesive unit, however, with the loss of F15 and joining of U22, it was identified as A2, and finally with the loss of U22 and joining of F23, identified as A3.)

In each of two captive flocks (A3 and D) interindividual responses were observed before and after injection of the subordinate male with 0.300 milligrams of testosterone propionate in 0.06cc of cotton seed oil every third day of the experimental period, for a total of three injections. Non-treated birds were handled and injected with 0.06cc cotton seed oil without testosterone propionate.

RESULTS

Sex Ratios

A difference in sex ratio was observed between flocks of adult birds and flocks of first year birds. In 9 of 10 flocks whose members had been present on the study area for one or more breeding seasons, the sex ratio was found to be 1:1 (Table 2). In order to examine the sex composition of flocks not in the study area and to attempt something of a control, four winter flocks were shot in January and February, 1969. These flocks were taken at distances ranging from 14 air miles to 60 air miles away from the study area. The sex of each bird was determined by dissection (Table 2). Flocks J, K, L, and M, which were taken at a distance from the study area, also were discovered to have a 1:1 sex ratio (Table 2). These birds were taken in January and February, 1969; therefore age by skull determination could not be used effectively. These flocks (J, K, L, and M) were assumed to be flocks of adult (not first year) birds because of their sex ratio.

Exceptions to the 1:1 sex ratio in flocks having adult members observed as follows: Flock A1 with a membership of four individuals (2 males and 2 females) consisted of only three individuals (2 males and 1 female) from 19 October, 1968 until 23 October, 1968, at which time a new bird became attached to the trio (Figure 2). Flock C1 numbering four individuals (2 males and 2 females) from 12 November, 1968 was observed to consist of only three

Table 2. Sex composition of winter flocks of Black-capped Chickadees from western New York

Flock	Males	Females	Unsexed	Total
A1	2	2	0	4
A2	2	1	1	4
A3	2	2	0	4
B	1	1	2	4
C1	2	2	0	4
C2	2	2	0	4
D	2	2	0	4
E	2	2	0	4
F	2	2	0	4
G	2	2	0	4
H[a]	3	2	0	5
I[b]	2	1	0	3
J[c]	5	5	0	10
K[c]	3	3	0	6
L[c]	2	2	0	4
M[c]	2	2	0	4

---

[a] Flock of first year birds observed in nature & captivity. Sex determined by Mosher-Lane Method (Appendix).

[b] Flock of first year birds in nature, observed through the breeding season. Sex determined by Mosher-Lane Method and substantiated by individual's breeding behavior.

[c] Flocks of Black-capped Chickadees shot outside the study area during the period 10 January -20 February, 1969. Sex determined by the Mosher-Lane Method and substantiated by dissection.

individuals (2 males and 1 female) until 14 November, 1968, at which time a new bird joined C1. Apparently these exceptions to the 1:1 sex ratio occurred as a result of the permanent loss of a female flock member. In each instance the missing female flock member was never seen on the study site again, and restoration of the 1:1 sex ratio by a new female bird took place in a relatively short time. Another notable exception occurred on 25 March, 1969. A first year bird (U20) attached itself to flock E, raising the membership to five and upsetting the 1:1 sex ratio. The new member (U20) traveled with flock E for 17 days and disappeared. Flock F had a similar occurrence on 3 April, 1969, with the new bird (U21) having a tenure of 15 days before disappearing.

These data indicate that the answer to the question, "is the sex composition of a flock of Black-capped Chickadees predictable or is it unpredictable?" is that resident flocks consisting of members which have experienced one or more nesting seasons are likely to be even numbered with a 1:1 sex ratio. This was true for 9 of 10 resident flocks (Table 2, A-G). Flock B, the possible exception, had an even number of birds; however, the sex of two members of the flock remained unknown (Table 2). Flocks of first year birds were likely to consist of uneven numbers causing the sex ratio to be unpredictable. However, both sexes were present in the two flocks of immatures studied.

Rank Order and Organization

The rank order in each of 11 flocks of adult birds (flocks A1, 2, 3, B, C1, 2, D, E, F, G) is illustrated in Table 3. In each of these flocks the alpha bird was a male. The mate of the alpha male was second in feeding order at the walnut. Data from my field notes is not sufficient to indicate an increase or decrease during the winter flocking period in the apparent feeding privilege accorded alpha's mate, with the approach of spring. The term "feeding privilege" is used here to denote the alpha male's refraining from chasing his mate away from the walnut when she is feeding in his presence. One might expect an increase in the incidence of alpha's mate exercising feeding privilege with the approach of spring and the breeding season; unfortunately I do not have sufficient data to support or reject such a conclusion.

In comparing hierarchies of Black-capped Chickadee flocks having a 1:1 sex ratio and retaining antecedent mates from past breeding season, to those of flocks of first year birds, it is noted that the alpha bird's mate (as previously described) often had precedence at a food source (feeding privilege). This arrangement was observed numerous times in flocks A1, A2, A3, and D. However, this was not observed in flocks H and I (with a membership of first year birds, which showed no evidence of pairing). In these flocks of first year birds, females were dominated by males and no evidence was apparent which suggested a female was accorded precedence in feeding at the walnut.

During January and February, 1969 a series of interesting events occurred. Flock C2 disbanded, with two of its members, M21 (alpha) and F3

Table 3. Hierarchies of free living Black-capped Chickadees as observed at a restricted food source

Flock	Alpha	Beta	Gamma	Delta	Epsilon
			1968-69		
A1	M2	F14	M13	F15[d]	
A2	M2	F14	M13	U22[d,i]	
B	M4	F12	U11	----	
C1	M21	F3	M1	F28[d]	
C2*	M21	F3	M1	F26[i,r]	
D	M11	F11	F13	M14	
			1969-70		
A3	M2	F14	M13	F23[i]	
D	M11	F11	F13	M14[o]	
E	M4	F21	M21	F3	
F	M1	F26	M24	F22	
G	M25	F20	M17	F19	
H	M20[i]	M22[i]	M23[i]	F24[i]	F25[i]
I	M27[i]	M28[i]	F27[i]		

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[d] Disappearance of F28, 29 October, 1968, of F15, 19 October, 1968, U22 found dead 29 November, 1968.

[r] Replacement of F28 by F26, 2 November, 1968.

[i] Refers to the members of the flock which were first year birds.

----Denotes an unmarked bird.

*Flock C2 disbanded sometime in January, 1969 (see Figure 2).

[o] Observed into January, 1970.

(his mate), observed traveling with M4 (alpha of 1968 flock B) and his mate (F21). Prior to my sighting of this quartet M4 and F21 were seen twice unaccompanied. Subsequent observations revealed that this quartet was indeed a cohesive flock and it persisted into the next winter. The alpha male (M4) of this new flock (E) was not supplanted by M21 in the 6 sightings of the foraging flock. Flock E was observed 18 times at the restricted food source and M4 supplanted M21 three times. Although M4 and M21 were both banded as adults it could be possible that M4 was the oldest resident of flock E. If this were so it might explain why he assumed the alpha position in flock E. The denotion of M21 to gamma in flock E cannot be explained in terms of M4's prior breeding territory being part of flock E's range. Reference to Figures 4, 5, 6, and 7 indicate that the range of flock E actually incorporated some of M21's prior breeding territory and is a distance from M4's prior breeding territory.

The other former members of flock C2 (M1 and F26) joined with M24 and F22 to form flock F. Little is known of M24 and F22's activities before observing them as members of flock F. In the 5 observations made of flock F at the restricted food source M1 supplanted M24 once. No other confrontations were observed, although M1 was noted as always being first at the walnut and never supplanted by other flock members. Only one observation was made of flock F foraging; therefore, no winter range could be established for this flock.

Tenure of Individuals on the Area

Figure 2 illustrates temporal and social relations of 28 Black-capped Chickadees which I was able to follow relatively closely over the period of their tenure on the study area. The number of months each of these chickadees was in evidence on the area (commencing with their initial banding) is presented in Tables 4 and 5. There were 18 birds banded in addition to those recorded in Figure 2. These birds could not be represented in Figure 2 due to insufficient data concerning their activities. Some were not seen again after banding, and may have been itinerants passing through the study area. Others were observed only occasionally and quite likely were from near-by woodland outside the study area. In addition to these birds there was a noticeable influx of unbanded birds in the autumn, mid-winter, and spring. It seemed as though some were looking for a flock to join or an area in which to stay; apparently finding no vacancy, they moved on (with exceptions recorded in Figure 2).

Flock Size

Winter flocks of resident birds observed in this study illustrated a relative constancy of membership, cohesiveness, synchronization of activity, and they generally seemed quite unified. Such flocks seldom exceeded four individuals. However, exceptions were observed from time to time. Family parties (i.e., newly fledged birds with parents) often exceeded this number, as did groups of first-year birds during the period of 8 July, 1969 to 4 August,

Table 4. Tenure of regularly observed male Black-capped Chickadees on the study area in western New York

Male	Month of Initial Banding	Flock to Which Bird Belonged	Age at Banding	Male's Rank in Flock[a]	Months on Area After His First Banding[c]
M2	Dec.	A1, A2, A3	Adult	Alpha	31[b]
M13	Dec.	A1, A2, A3	Adult	Beta	30[b]
M4	Dec.	B, E[d]	Adult	Alpha	27
M21	Feb.	C1, C2 E[d]	Adult	Alpha Beta	26
M1	Dec.	C1, C2 F[d]	Adult	Beta Alpha	22
M11	Mar.	D	Adult	Alpha	22
M14	Mar.	D	Adult	Delta	21
M24	Mar.	F	Adult	Beta	16
M25	Mar.	G	Adult	Alpha	8
M17	Oct.	G	Immat.	Beta	12
M20	Oct.	H	Immat.	Alpha	6
M22	Oct.	H	Immat.	Beta	6
M23	Oct.	H	Immat.	Gamma	6
M27	July	I	Immat.	Alpha	12[b]
M28	July	I	Immat.	Beta	12[b]

[a] Details of flock membership can be ascertained from Figure 2.

[b] Individuals known to be on the study area and alive at termination of study June, 1970.

[c] Average time on the area 15.2 months; range 6 to 31 months.

[d] Shift in flock membership, apparently due to disappearance of some flock members.

Table 5. Tenure of regularly observed female Black-capped Chickadees on the study area in western New York

Female	Month of Initial Banding	Flock to Which Bird Belonged	Age at Banding	Female's Among Other Females in Flock[a]	Months on Area After Her First Banding[c]
F14[d]	Dec.	A1, A2, A3	Adult	Alpha	30[b]
F15	Dec.	A1	Adult	Beta	10
F23	Sept.	A3	Immat.	Beta	18[b]
F12[d]	Dec.	B	Adult	Alpha	12
F3[d]	Dec.	C1, C2	Adult	Alpha Beta	28
F28	Mar.	C1	Adult	Beta	4
F26	Oct.	C2, F[e]	Immat.	Beta	12
F11	Mar.	D	Adult	Alpha	22
F13	Mar.	D	Adult	Beta	22
F21[d]	Dec.	E	Adult	Alpha	16
F22	Mar.	F	Adult	Beta	16
F20[d]	Mar.	G	Adult	Alpha	8
F19	Mar.	G	Adult	Beta	8
F24	Oct.	H	Immat.	Alpha	6
F25	Oct.	H	Immat.	Beta	6
F27[d]	July	I	Immat.	Alpha	12[b]

[a] Details of flock membership can be ascertained from Figure 2.

[b] Individual known to be on the study area and alive at termination of study June, 1970.

[c] Average time on the area 14.3 months; range 4 to 30 months.

[d] Alpha male's mate and usually second to feed at restricted food source.

[e] Shift in flock membership.

1969. These bands ranged in size from 4 to 10 birds. The numbers of birds in these bands shifted frequently, and banded young were likely to be seen any place throughout the study area.

VanTyne (1928) reported witnessing a flock of 50 chickadees on 20 May, 1928 in the daytime. Apparently this horde had grouped together in migrating from Sand Point to cross Saginaw Bay, Lake Huron. A migrating flock of Black-capped Chickadees on 7 September, 1968 in Lincoln County, Maine, numbering in excess of 100 was counted by Bagg (1969). Butts (1931, 9) stated that it is ". . . well known, Chickadees travel about during the fall and winter in small groups or flocks. The number of birds seen together may be anywhere from two to fifty or sixty."

In addition to migratory movements, apparently a food source (especially a concentrated one such as a feeder) can affect the size of the flock. Butts (1931, 12-13) reported that upon allowing all but one feeding station to be without food from 3 February to 26 February that two flocks merged to form one flock of 22 birds. This flock of 22 birds did separate into its original flocks of 10 and 12 birds, occasionally. In this context Butts (1931) does not mention whether or not these flocks of 10 and 12 separated into smaller units during the period. However, he does mention in his study observing flocks numbering less than eight Black-capped Chickadees. It seems to me that in reporting on the merging of the two flocks Butts used the term flock rather loosely. From his description the "group" of 22 did not demonstrate a constancy of membership and cohesiveness which I believe it should have to merit the term "flock." Odum (1942, 507) stated of the Black-capped Chickadee "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 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 hour to hour." From comments by Hinde (1952) concerning flocking behavior of the Great Tit (Parus major) and Odums's (1942, 507) statement that "Even in winter when most individuals remain within remarkably limited ranges flocks break up and reform or individuals pass from one flock to a neighboring one . . . ," I would expect flocks to merge, and perhaps break up later. However, I could not clearly discern merging of flocks on my area. I did see what might be called "overlapping" many times at the original feeder (Figure 3). For example "stragglers" of flock A1, were beginning to move toward trees in the direction of the alpha bird's departure as another of the flocks in the area was moving through the trees toward the feeder. The last members of flock A1 would usually be out of the immediate vicinity of the feeder when the second flock began to feed.

Optimum flock size seems to depend on local ecological conditions and the time of the year. In this study the consistent resident flock size was four. Occasionally what Odum (1942) described as congregations of more than four birds would occur around the original feeder (if the other feeders as shown in Figure 4 were empty) in the coldest days of the winter months.

Occasionally as many as 10 birds might be seen in the vicinity of the feeder. In these instances only one flock of four would be feeding on seeds which had fallen from the feeder to the ground. Other birds would be in the near-by trees and "take turns" darting to the feeder, acquiring a seed and darting back to a tree. I do not consider this type of activity to constitute merging of flocks. Flocks seen away from the vicinity of the feeder whose members were foraging on naturally occurring food consisted of four birds, with the exceptions which have been noted in the foregoing text.

Flock Membership

Some of the events which influenced flock composition on the study area were presumed predation, emigration, temporary attachment of itinerants and the brief duration of attachment of fledged offspring to the mated pair. Winter flock A1, composed of adults M2, F14, M13 and F15, observed through one breeding season, changed in membership when the subordinate male's mate (F15), disappeared 19 October, 1968. Shortly after the disappearance of F15, a known first year bird, U22, left a flock of first-year birds and joined with M2, F14, M13 to form the quartet designated as A2. The new bird occupied F15's old position in the hierarchy as the subordinate in the flock. On 29 November, 1968, U22 was found dead. Another first-year bird, F23 (previously observed 2 January, 1969, in the company of U23 (previously observed 2 January, 1969, in the company of U23, U24 and an unbanded chickadee), left

Figure 3. Approximate winter ranges of flocks A1, B,C1, the rectangle encloses the area of the original feeder established 28 December, 1967. Legend for vegetation as in Figure 1.

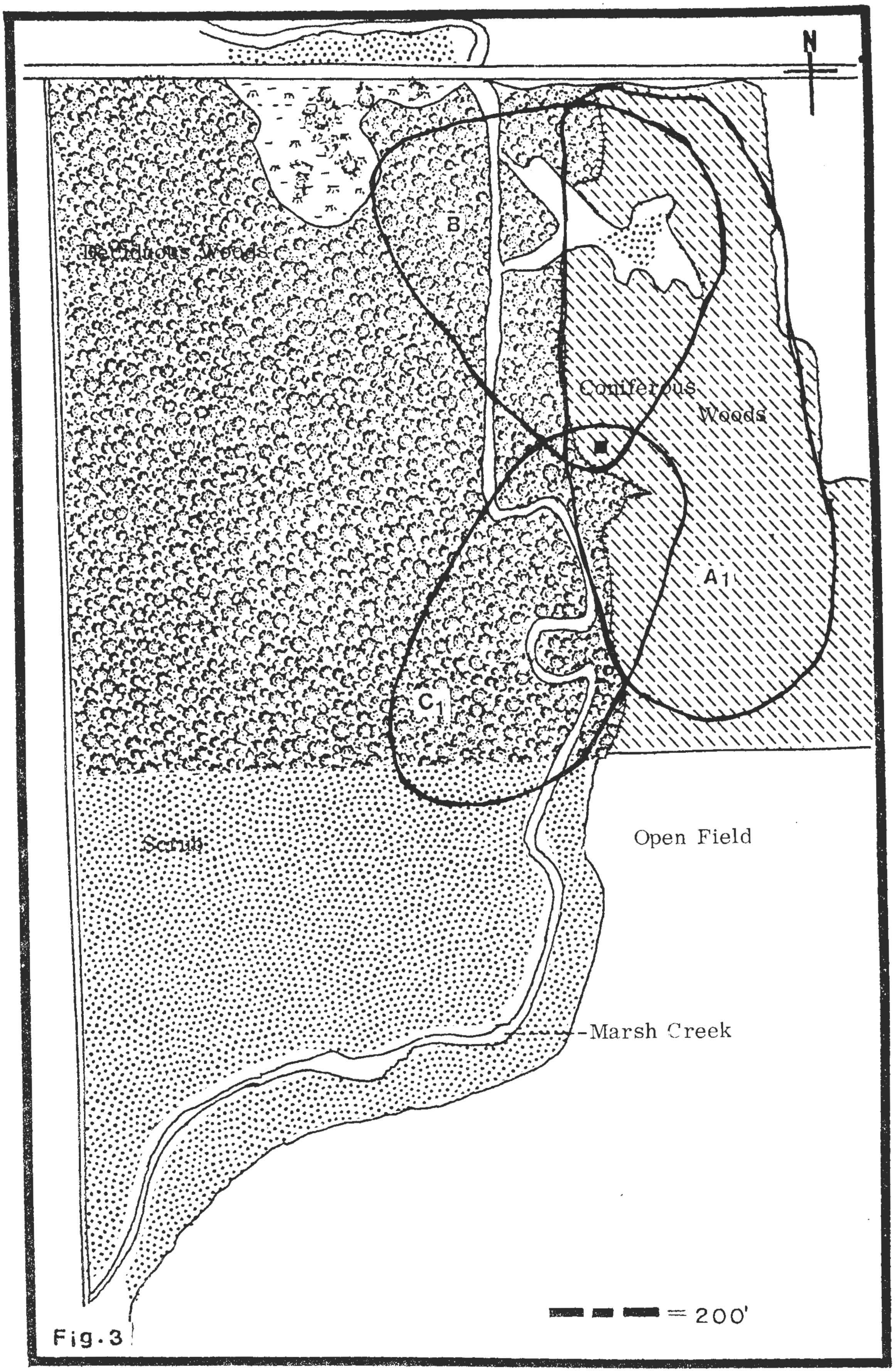
N
B
Deciduous Woods
Coniferous Woods
A1
C1
Open Field
Scrub
Marsh Creek
= 200'

Fig. 3

Figure 4. Approximate winter ranges November, 1968-March, 1969, of flocks A1, C2, D, E, G. The rectangle represents the original feeder established December, 1967. Triangles represent subsequent seed dispensing feeders added December, 1968. Legend for vegetation as in Figure 1.

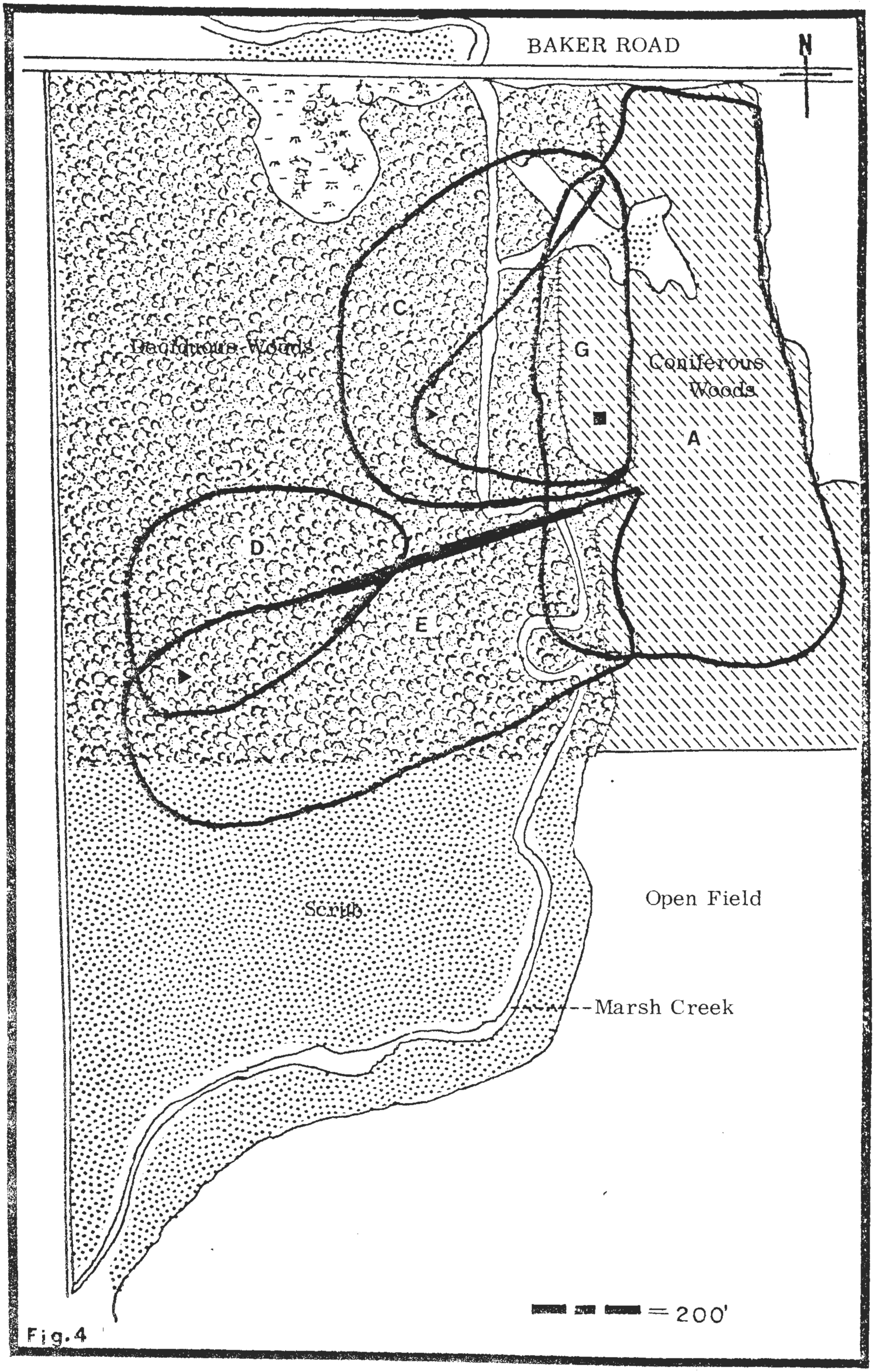
BAKER ROAD
N
Deciduous Woods
Coniferous Woods
C
G
A
D
E
Scrub
Open Field
Marsh Creek
= 200'

Fig. 4

the flock of first-year birds and joined M2, F14, M13, 5 January, 1969 in the subordinate position previously occupied by U22, to form flock A3.

The two individuals which joined the remaining members of flock A1 in 1968 and 1969 came from a group of five birds. Four members of this flock were banded 23 August, 1968, and determined by lack of skull pneumatization to be first-year birds The fifth member of this group remained unbanded and age unknown. This flock of birds was seen only three times after banding. On 15 October, 1968 they were seen at the original feeder (Figure 3), with the departure of U22 occurring soon afterward. The next sighting was on 2 January, 1969 in a woodland 250 yards north of the study area prior to the departure of F23. At this sighting only four birds were in evidence (U 23, U24, F23) and an unbanded individual (it is assumed that U22 had not been replaced in this flock because only the four birds were seen at this time). The final sighting of U23 and U24 was 26 February, 1969. At this time U23 and U24 were traveling with two unbanded birds (F23 having joined flock A3). The three sightings of these birds produced no data which would give insight into their hierarchy. F23 mated in the spring of 1969 with M13 (Figure 7), and has retained its place in flock A3 since joining 5 January, 1969 (Figure 2).

Flock C1 had a similar history, except that one bird (F28) disappeared about 13 November, 1968. Again this was the mate of the subordinate male and again replacement came from a flock of first-year birds (U25, U26, F26), all banded 2 November, 1968. At the time of banding these birds were determined to be first-year by the skull-pneumatization method. No member of this flock was again in evidence until 27 November, 1968, when F26 joined flock C2. She mated with M1 the following spring (Figure 2) (U25 and U26 were never seen again). I could not detect whether the "widowed" beta birds of flock A1 and flock C1 left the area in search of a mate or whether the female from the immature flock joined the flock of adults without special solicitation. Because of the tendency of first-year birds to be less sedentary and range more freely over the area I presume contact with and subsequent attachment to flock A1 and C1 (of U22 and F26 respectively) occurred as a result of the free movement of the young flock.

Of all the flocks observed during the study, flocks A1, A2, and A3 had the most stable membership. The alpha bird (M2), his mate (F12) and the beta male (M13) were members of the flock during three successive winters (1968, '69, and '70).

Removal of the Alpha Bird

To ascertain the responses of individuals and the flock to the alpha bird's absence, temporary removal of the alpha bird from flocks A3, D, and E, for approximately 30 hours was accomplished on 1, 3, and 5 January, 1970, respectively. Members M2, F14, M13 of flock A3 had been observed on the study area since January, 1968; flock D, since December, 1 968; and flock E, since February, 1969. Thus, behavior patterns of the intact flocks were known previous to alpha's removal. Immediately following the alpha's removal, the common response of the remaining individuals appeared to be one of confusion or perhaps searching. The birds flew from tree to tree, hopped about through the branches and gave loud "chickadee dee" calls. Because of their rapid movement I could not be sure which, if any, other birds in addition to alpha's mate were calling. Odum (1942) noticed this type of calling when mates were separated.

In flock A3, M13 the beta male, seemed to assume the alpha position in approximately 10 minutes after alpha's removal. The first indication of M13's new role was that he supplanted F14 twice at the walnut (nut location near feeder, Figure 5). Approximately 20 minutes later M13 was seen to chase F14 (alpha's mate) from a branch near the walnut. Such a confrontation between M13 and F14 had not been observed in the previous two years of their occupancy. Dixon (1965) describes a similar incident occurring in Mountain Chickadees upon removal of the alpha male from the flock. The next day, 2 January, M13 was first at the nut while F14 and F23 stayed in the tree branches near-by. The alpha bird, M2, was returned to the study area later that day (Table 6). At the time of his release flock A3 was not in evidence. Neither M2, nor flock A3 was observed that day. On 3 January, 1970, M2 was with the flock as before. No confrontations between M2 and M13 were observed and as far as could be detected all was as before the alpha's removal.

On 3 January, M11, the alpha male of flock D, was removed. Later, the alpha's mate (F11), dominated the walnut (in the sense that she was

Table 6. Summary of events following removal of the alpha male

Flock	Time of alpha's removal	Period of subsequent observation	Immediate response	Later consequence	Time of restoration of alpha	Date normal behavior resumed
A3	1/1/70	2 hours	Loud chickadee call. Much activity.	M13 dominant at nut; supplants F14	1/2/70 2;20 pm flock not in view	1/3/70 9;30am
D	1/3/70[b] 10:30 a.m.	5 1/2 hours[a]	same as above	F11 dominates nut suppl. F13	1/4/70 3;30 pm Flock not in view	1/5/70 2:15pm
E	1/5/70 8:35am	6 1/2 hours[a]	Loud chickadee call. Very active. Flew off without feeding. Not seen again until 1:17pm.	Beta male M21 dominates nut. Chases F21, alpha's mate from nut.	1/6/70 2:45pm Flock not in view.	1/7/70 11;15pm

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[a] Flock seen intermittently at the feeder.

[b] Temporal pattern of flock D interrupted during alpha's absense. However, it returned to former pattern 5 January, 1970 (the day after alpha's restoration).

undisturbed by others while she fed). The next morning I saw F11 supplant F13 from a branch near the walnut but no other confrontations were observed. M14, the subordinate male individual in the flock, remained retiring as he had done before the alpha male was removed. In no manner was M14 observed to assert himself in the alpha's absence. There was no observed confrontation between the alpha's mate (F11), and M14. F11 clearly was dominant at the walnut, as well as arriving first to the feeding area. However, the temporal pattern of visitation to the feeder changed during the alpha's absence. Before alpha's removal flock D was usually at the feeder (Figure 5) between 8:45 and 9:30am and again about 11:00am. After alpha's removal there seemed to be no set time, or at least no pattern was apparent, when flock D would arrive at the feeder. However, the day after the alpha's release the flock again arrived at the feeder approximately in keeping with the pre-removal pattern (Table 6). These observations imply that M11's presence influenced the temporal pattern of the flocks visit to the feeder. M11 was returned to the area at approximately 10:00am 4 January, 1970. Flock D was not in evidence at the time of his release and was not seen again until the next day.

On 5 January, 1970, M4, the alpha male of flock E, was removed. The remaining flock members, F21 (alpha's mate), F3, and M21, became quite active. They flew from tree to tree around the feeding area (Figure 5), hopping from branch to branch of various trees, calling "chickadee dee" loudly. After about 10 minutes of this activity the three birds then left the

Figure 5. Approximate winter ranges November 1969-March 1970 of flocks A3, D, E, H, I. The rectangle represents the original feeder established December, 1967. Triangles represents subsequent seed dispensing feeders added December, 1968. Legend for vegetation as in Figure 1.

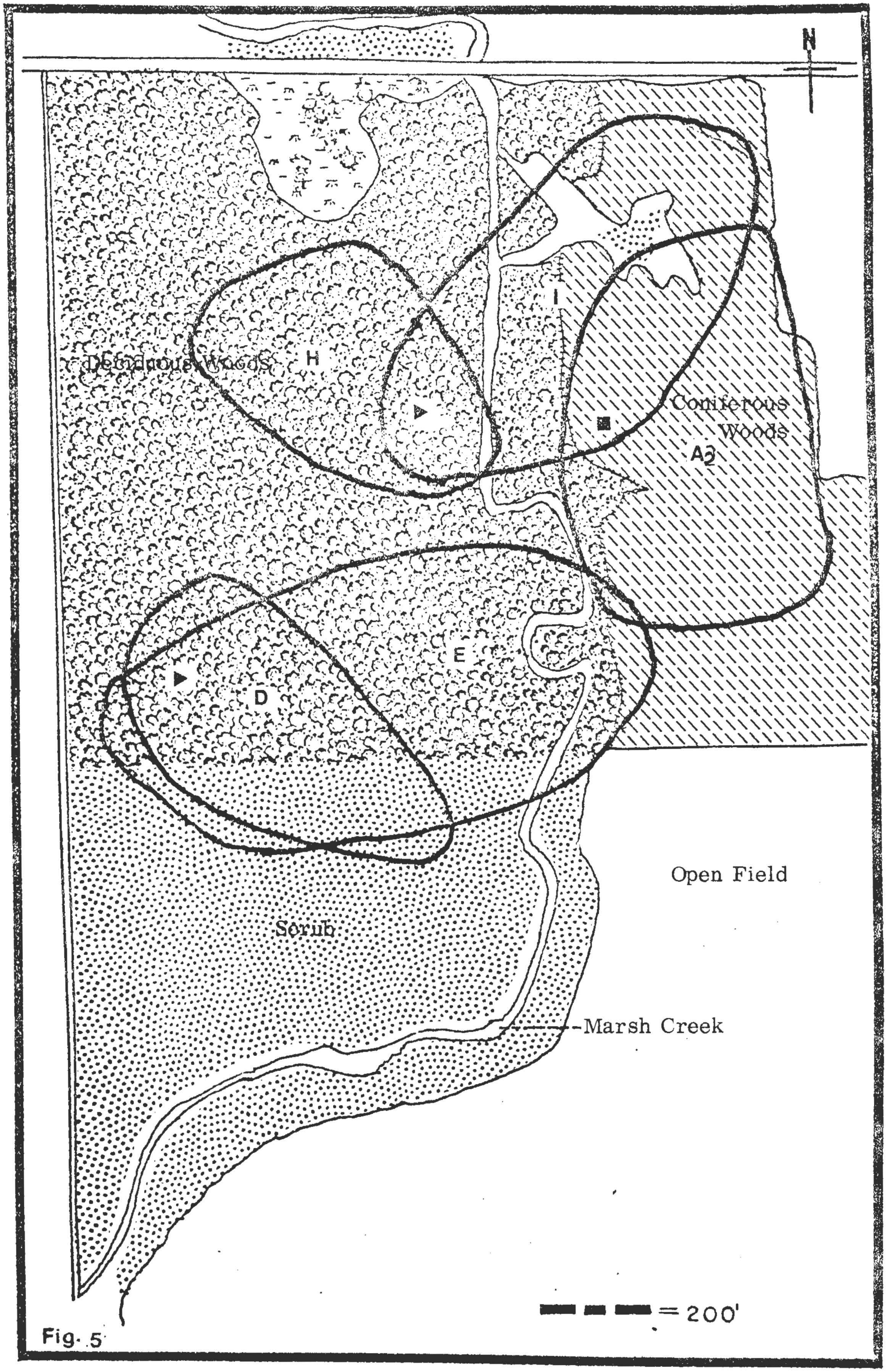

N
Deciduous Woods
H
I
Coniferous Woods
A_2
E
D
Open Field
Scrub
Marsh Creek
= 200'

Fig. 5

area of the walnut, without feeding. Loud "chickadee dee" calling could be heard in the direction of their departure. However, it was impossible to follow and make observations, because of the deep snow and the swiftness of their movement away from me through the trees. Flock E was not seen again until 1:17pm that afternoon (Table 6). The feeding area remianed under surveillance during the interim (i.e., 8:35am-1:17pm). Usually flock E would make frequent visits to the feeding area throughout the morning and late afternoon. The beta male (M21), was first to the walnut upon flock E's return at 1:17pm, while F3 and F21 lagged. As the beta male fed, F3 and F21 flew about the area perching in the branches of the adjoining trees. When the alpha bird (M4) was present they would wait in near-by trees with little activity. Beta male (M21) supplanted the alpha's mate (F21) from a branch near the walnut giving the "slee slur" ("fighting call," Dixon and Stefanski, 1970) while simultaneously raising and lowering his crest. F21 then flew to a branch in another tree about 15 yards away from the site of the altercation. After landing on the branch, F21 appeared to be looking for food as she examined cracks in the bark and frequently "bill wiped." No other confrontations were observed among the trio. The next day, M4, the alpha male, was released into the study area. No birds were in the vicinity at the time of his release. Neither he nor any of his flock mates were observed that day. The next day (7 January, 1970) flock E was observed at 11:15am near the walnut (near the feeder as shown in Figure 5). They proceeded to the nut with M4 (alpha) reaching the nut and feeding first. They remained in area 15 minutes, and in that time no confrontations were observed. Subsequent observations (through March, 1970) of this flock revealed no change in the hierarchy.

These data indicate that removal of the alpha male results in temporary disruption of the flock organization. The immediate reaction of the remaining flock members appeared to be confusion or searching for the alpha. In two of the three instances, the alpha's mate seemed to lose her status or at least did not enjoy precedence at the restricted food source as she had when her mate was present. In two out of the three flocks (A3 and E) the beta male appeared to assume the dominant role vacated by the alpha male. It would seem that the dominant bird s presence promoted flock stability, but it is difficult (from my observations) to determine the actual extent of leadership given by the alpha bird. However, change in routine of flock D, is indicative of the alpha's influence.

There were no observed interactions between the experimental flocks (those with alpha male temporarily removed) and the other "intact" flocks. Therefore I do not know if the "intact" flocks could have excluded the experimental flocks from the feeder.

The leadership of the alpha bird was not strongly expressed in the sense of actually leading the flock. It was noted numerous times that the alpha bird was not always the first chickadee to arrive at the restricted food source. Allee (1942, 160) commented that the socially dominant animals may or may not be the leaders in their groups. In commenting on domestic chickens he stated "The alpha hen in a penned flock does not necessarily lead in foraging expeditions when the hens are turned out into an open lot. In fact, in such a foraging flock leadership changes frequently . . . ." However, upon the arrival of the dominant Black-capped Chickadee in the flock which I observed, any other flock member which might be feeding at a walnut would relinquish his position upon alpha's arrival, or be quickly supplanted by the alpha.

Effects of Additional Feeding Stations

A considerable amount of the literature reporting patterns of behavior in the genus Parus cites observations made at winter feeding stations. I thought it might be wise to establish a seed dispensing feeder, to enable me to compare the actions of the chickadees on the study area with the behavior of chickadees reported in this literature. On December 28, 1967, a seed dispensing feeder was placed in the coniferous woods approximately 35 feet in from the boundary of the deciduous-coniferous woodland (Figure 3). Unfortunately other duties at the time prevented me from observing regularly the first week in which the feeder was supplied with sunflower seeds. In the second week a relatively large number of unbanded chickadees was frequenting the feeder. Until the establishment of the feeder the only birds I had regularly detected in that area of the conifers were ones which I had banded previously (Figure 2). After banding many of the "new" birds and following their movements, I discovered that they ranged over an area west and somewhat south of the coniferous woods. Figure 3 illustrates the ranges of the flocks observed 1 January through 30 March, 1968.

In December, 1968, two additional seed dispensing feeders were installed (Figure 4). When these newly installed feeders had sunflower seeds in them, flocks D and C2 were not in evidence at the original feeder located in the conifers. However, when the newly established feeders were left empty for 2 or 3 days, flocks D and C2 would visit the original feeder. Flocks A2 and later (i.e., January, 1969) A3 and G used the original feeder almost exclusively; however, flock G was not seen as frequently at the original feeder when the new feeder 300 feet directly west of the original feeder (Figure 4) contained seeds. Continued observations produced the approximate flock ranges illustrated in Figure 4.

From December, 1969, to March, 1970, flocks A3, D, E, H, and I, used the original feeder when the two later established feeders were empty. When the two newly established feeders were provided with seeds, they were utilized by those flocks having ranges in that area (Figure 5).

With the relatively heavy utilization of the original feeder when the other feeders were empty, considerable interflock friction might be expected. Dixon (1965, 297) reported altercations between alpha males in flocks of Parus gambeli. He described such interflock contests as being characterized by ". . . prolonged and strenuous pursuit flights in which the female and subordinate males were chased by males of the opposing flock; (2) challenges of the bird perched on the pendant feeder . . . ; and (3) obvious attempts of the "defending" male to stand between his adversaries and the food." No interflock encounters similar to the skirmishes described by Dixon (1965) were revealed in the various times (totaling approximately 17 hours) that two or more of the flocks were in evidence at the feeder or in the near-by area. Mutual avoidance rather than clashes was the usual occurrence. It is possible however, that such contests could have taken place at times when the birds were not under observation.

The flocks on the study area did not use the origianl feeder at the same time. Occasionally there was overlapping (as described in the section on flock size). "This awareness of boundaries was manifest in the avoidance of trespass if a feeding station in the range of another flock was occupied." This statement by Dixon (1965, 297) describes what I also observed at the feeders. The following is a typical example of this flock activity. On 8 March, 1969, flock C2 quickly left the area of the original feeder as flock A3 approached. No skirmish was seen, the individuals of flock C2 seemed to know they were trespassing in flock A3's range, and readily relinquished their position at the feeder. As described on page 31, as many as 10 birds would be seen in the vicinity of the feeder. In these observations it is interesting to note that I have recorded birds from flocks C2, D and E engaged in "taking turns," while I have nothing in my field notes regarding flock A3 performing this type of activity. I conclude from the data that birds from other ranges than flock A3's are on neutral ground and are relatively tolerant of one another. However, these non-residents tend to move away from the feeder at the approach of the flock on whose range they are trespassing.

Thus, the establishment of a seed dispensing feeder in the winter of 1967-1968 attracted unbanded birds into flock A2, A3's range. The birds using the feeder within the range of flock A3 were discovered to have foraging ranges to the northwest, west and southwest of the feeder respectively. Flock A3's range was apparently respected, as was noted by the example given in the preceding paragraph. When other feeders were established within the various other flock ranges, they were readily utilized, and flock A3's range was rarely violated. Trespass on flock A3's range did occur when the feeders outside of flock A3's range were empty and the feeder within flock A3's range had seeds. Unfortunately time and lack of manpower did not permit me to make extensive observations at other feeders to determine if a similar situation of respect for range developed at other feeders. I could not detect any parallel to Brian's (1949) findings in the Great Tit of decreasing dominance further from the home area.

The lack of extensive strife between flock A3 and the other flocks using the feeder within flock A3's range would seem to indicate a flexibility of flock range boundaries. This flexibility seemed aided by the temporal patterns established by the various flocks using the original feeder. The advantage to the survival of the individual and consequently to the species, in terms of energy conserved by reduced conflict and food gained, in the severe winters of the area, is obvious.

The Confined Flocks

Three flocks were studied in the aviary. Flock D was thought to be a recent assemblage of individuals because I could not clearly establish that they were a cohesive flock until late October, 1968. However, the members had bred on the study area during the preceding breeding season. Little was known about the activities of the individuals that became flock D, before the 1968 breeding season. They were observed in the wild as a flock from 28 October, 1968 and rather intensively 25 January to 4 February, 1969 (just prior to their capture and confinement). This flock was studied in the aviary from 5 February, 1969 to 5 March, 1969. Flock H, a group of 5 first-year birds, was observed as a flock from November, 1969, and intensively 19 January to 4 February, 1970 (just prior to their confinement). This flock was studied in the aviary from 4 February to 7 March, 1970. Flock A3 (three of its members--M2, F14 and M13--observed as flock A1, A2, since January, 1968) was observed from January, 1969, and intensively from 20 February to 7 March, 1970 (just prior to their confinement). This flock was observed in the aviary from 7 March to 26 March, 1970. Prior to their captivity their hierarchies were reassessed (Tables 7, 8, 9).

In each flock the hierarchy remained the same in captivity as that observed in the field (Tables 7, 8, 9). In flocks A3 and H, dominance at a food source, at times, was not clear cut. However, in time the retention of the original heirarchy was substantiated by definite supplants and retreats.

Table 7. Dominance relationship in flock A3, free living and captive[a]

	M2	F14	M13	F23
		Free Living[b]		
M2	--	1	--	1
F14	--	--	2	1
M13	--	--[c]	--	1
F23	--	--	--	--
		Captive[d,e]		
M2	--	2	5	3
F14	--	--	3	7
M13	--	--	--	3
F23	--	--	1	--

---

[a] The number of contests won by individuals listed at the left may be read in horizontal columns.

[b] Observed 20 Feb -Mar., 1970, total observation time 10 hours.

[c] M13 chased F14 when M2 was removed (described in text).

[d] Observed 7 Mar.-26 Mar., 1970, total time observed 10 hours.

[e] Observations completed before subordinate male received testosterone propionate treatments.

Table 8. Dominance relationships in flock D, free living and captive[a]

	M11	F11	F13	M14
		Free Living[b]		
M11	--	1	3	--
F11	--	--	5	4
F13	--	1	--	8
M14	--	--	--	--
		Captive[c,d]		
M11	--	3	7	2
F11	--	--	9	5
F13	--	--	--	3
M14	--	--	--	--

---

[a] The number of contests won by individuals listed at the left may be read in horizontal columns.

[b] Observed 25 Jan.-4 Feb., 1969, total observation time 15 hours.

[c] Observed 5 Feb.-5 Mar., 1969, total time observed 17 hours.

[d] Observations completed before subordinate male received testosterone propionate treatments.

Table 9. Dominance relationships in flock H, free living and captive[a]

	M20	M22	M23	F24	F25
			Free Living[b]		
M20	--	10	9	6	3
M22	--	--	15	5	2
M23	--	--	--	3	1
F24	--	--	--	--	11
F25	--	--	--	1	--
			Captive[c,d]		
M20	--	17	11	7	4
M22	--	--	16	5	9
M23	--	--	--	10	6
F24	--	--	--	--	14
F25	--	--	--	3	--

[a] The number of contests won by individuals listed at the left may be read in horizontal columns.

[b] Observed 19 Jan.-4 Feb., 1970, total observation time 15 hours.

[c] Observed 4 Feb.-7 Mar., 1970, total observation time 15 hours

[d] Observations in captivity never included treatment of any flock member with testosterone propionate.

Removal of the alpha male for two hours from each captive flock resulted in two cases (flocks A3 and H) in the beta male assuming the dominant role. Upon alpha's removal there was a considerable amount of "chickadee dee" calling in the aviary. Unfortunately no record was made indicating which bird or if all the remaining birds were giving the call. Approximately 20 minutes after alpha bird's removal the remaining members of the flock seemed to settle down. The beta birds initiated feeding and movement in the aviary as well as dominating the food source at will. In flock D, F11 (alpha's mate) seemed to assume the dominant role in a manner similar to that of the beta birds (i.e., males) of flocks A3 and H. The subordinate male of flock D (M14), remained shy and retiring as he had in the wild before and after alpha's removal.

Androgen Treatment of Subordinate Males of Captive Flocks

The subordinate males of flocks A3 and D were injected with 0.300 milligrams of testosterone propionate in 0.06cc cotton seed oil. The 17 hours and 47 minutes of observation before the injection of M14 indicated that there was a well defined hierarchy in flock D (M11 alpha, F11 beta, F13 gamma and M14 delta). M14 behaved in a most retiring manner. No confrontations with other flock members were observed in which M14 attempted to assert himself in the wild or in captivity. After M14's treatments with testosterone propionate, there was a definite increase in his general flight activity as well as his movements among the branches of the wood plants in the aviary

(Table 10). He also appeared most reluctant to retreat upon the approach of the other members of his flock, although prior to treatment he readily retreated from these birds. The day after treatment, actual confrontations and supplants increased among all members of the flock (Table 10), and an apparent breakdown of the flock organization occurred. Although M14 (the subordinate male) did not become the dominant figure, he did seem to precipitate disorganization (or at least disruption) in a rather stable, well organized flock.

Flock A3 with three of its members having been flock mates and observed in the field from January, 1968, until March, 1970, and the fourth member (F23) joining in 1969 replacing M13's deceased mate (Figure 2). M13, the subordinate male, was in his third winter as a flock member with M2, and F14. The hierarchy in the aviary remained the same as that observed in the field (Table 7). After M13 was injected with testosterone propionate, an increase in general flight activity, as well as movement through the branches of the woody plants in the aviary, was noted. Other than this, there was no significant change noted in his interactions with the others (Table 10). The flock hierarchy remained exactly the same as before captivity, with little disturbance to other flock members (Table 7).

A statistically significant difference was noted in the reaction of flock A3 and flock D after the subordinate's treatment with testosterone propionate. A formula from Guilford (1956) was employed to determine differences between changes for uncorrected samples (Table 11).

Table 10. Summary of aviary observations

	Before[a]			Before[a]		
	Flock D	Flock H[b]	Flock A3	Flock D	Flock H[b]	Flock A3
Total Observation Time in the Aviary (hrs. & min.)	17:47	15:00	12:00	17:31	15:00	10:00
*Average Encounter Rate Per Hour of Subordinate Male with Alpha Male	0.411	0.754	0.504	2.79	0.748	1.58
Significance df 16	--	--	--	$P = .01$	n.s.d.	$P < .05$
*Average Rage Pooled Encounter Rate per Hour Among Flock Members excluding Subordinate Male	6.0	9.1	4.0	22.0	8.3	4.7
Significance df 4	--	--	--	$P = 0.1$	n.s.d.	n.s.d.

[a] Treatment of the subordinate male with testosterone propionate.

[b] No member of this flock was treated with testosterone propionate.

* Differences between means of pre-and post-testosterone propionate treatment were tested by non-paired t-tests.

Table 11. Differences between changes for uncorrected samples comparing flock A3 with flock D*

	Flock D	Flock A3
Average encounter rate per hour pooled before and after treatment with testosterone propionate	14.0	3.4
Significance		P 0.001
df 6		

---

*Using the formula from Guilford (1956)

$$t = \frac{Me_1 - Me_2}{\sqrt{\alpha m_1^2 + \alpha m_2^2}}$$

Where Me_1 = mean of encounters between M11, F11, F13 post-testosterone propionate injection minus the mean of pre-testosterone propionate injection of flock D.

Me_2 = mean of encounters between M2, F14, F23, post-testosterone propionate injection minus the mean of pre-testosterone propionate injection of flock A3.

αm_1 = standard error of mean of first distribution.

αm_2 = standard error of mean of second distribution.

Miscellaneous Observations

Hoarding was frequently observed in the aviary when an overabundance of food was made available. The alpha bird and his mate would dominate the food source initially. Eating until they seemed satiated, they (alpha and his mate) would continue to take food and cache it in any available crevice. While these birds were busy caching the birds subordinate to them would go to the food source. Often the subordinate birds would leave with no food if the alpha or his mate returned too quickly. While the alpha and his mate were busy at the food source or occupied in caching food, the subordinate birds would steal from the dominant birds' caches. Occasionally a subordinate bird would be caught in the act of stealing and be driven off by the dominant bird either giving a "fighting call" (occasionally accompanied by crest raising) or chasing the thief. Stealing from the dominant bird's cache was common practice among subordinate birds in all flocks observed in the aviary.

Caching of food by Black-capped Chickadees was also practiced in the wild. This caching was often observed immediately after the seed dispensing feeders had been filled. The pattern followed that observed in the aviary. However, I was unable to observe all the interactions between individuals as I could in the aviary. It is assumed that the pattern of behavior observed for subordinate birds, that is finding other bird's caches and utilizing them, was practiced in the wild.

The fate of U22 was revealed when its bands were discovered among the contents of a great Horned Owl (*Bubo virginianus*) pellet.

Breeding Territories

Establishment of breeding territories was first detected in the latter part of April each year. The date at which time territories were seriously defended varied each year of the study. This variance seemed due to weather patterns. For example a cold snap of a week or so would tend to inhibit such activity. Warm weather bringing on buds seemed to stimulate this activity.

Brewer (1963, 21) cited numerous sources estimating territory size of the Black-capped Chickadee. He gave these estimates equal weight whether the size of one territory or a mean for several was given. Brewer stated that "The resulting mean and standard error (N = 12) were 3.64 ± 0.96." The territory size to which Brewer alludes is recorded in acres. In this study the average size of the 12 territories measured in late May during the nest building stage incorporating coniferous woods for 1968, 1969 and 1970 was 3.0 acres, with individual pair territories ranging from 2.3 acres to 4.1 acres. The 9 territories measured in late May during the nest building stage, for the same years, in the deciduous woods, averaged 3.4 acres, with individual territories ranging from 2.2 acres to 3.5 acres. Stefanski (1967) in Utah measured territories for the Black-capped Chickadee during the nest building stage and found an average of 5.4 acres.

The chickadees excavated nesting holes in dead elms. Although there are dead elms scattered throughout the deciduous woodland, a preponderance of dead trees is located in the spring flood areas of the creek and its banks. Approximately 75 percent of the dead trees in the flooded area are elms. The other dead trees are of various species also represented in the contiguous deciduous woodland. All nests that were located were found in dead elms near the creek banks or in areas flooded by the creek (Figures 6, 7, 8).

Trautman (1940) recorded that Carolina Chickadees (*Parus carolinensis*) excavated rotten wood for nesting holes. Bond (1957) found that the highest number of Black-capped Chickadee nests were found in pioneer stands of woods (in southern Wisconsin), where there were more soft wood trees. The chickadee seems to prefer soft or rotten wood for excavating. Klyver (1961, 549) alludes to this, commenting on the Black-capped Chickadee's ". . . instinctive drive of digging a hole in soft wood." This preference could explain the heavy concentration of nest sites (and suspected nest sites) in the area of the woods having the highest concentration of dead wood. The fact that this area floods could also be a contributing factor to its popularity with nesting chickadees. Aldrich (1943, 398), alluding to the fluctuation in the abundance of breeding birds which occurred in a hydrarch community, stated "This amazing fluctuation coincided with the water content of the substratum that was in part dependent upon the spring and summer rainfall . . . ." The

Figure 6. Dispersion of chickadee territories and nesting sites during the 1968 breeding season.

The dashed lines enclose the approximate boundaries of the territories chickadee pairs held. The number identifies the pair nesting on the territory (see Figure 2). The large black dot, indicates nest location.

Legend for vegetation as in Figure 1.

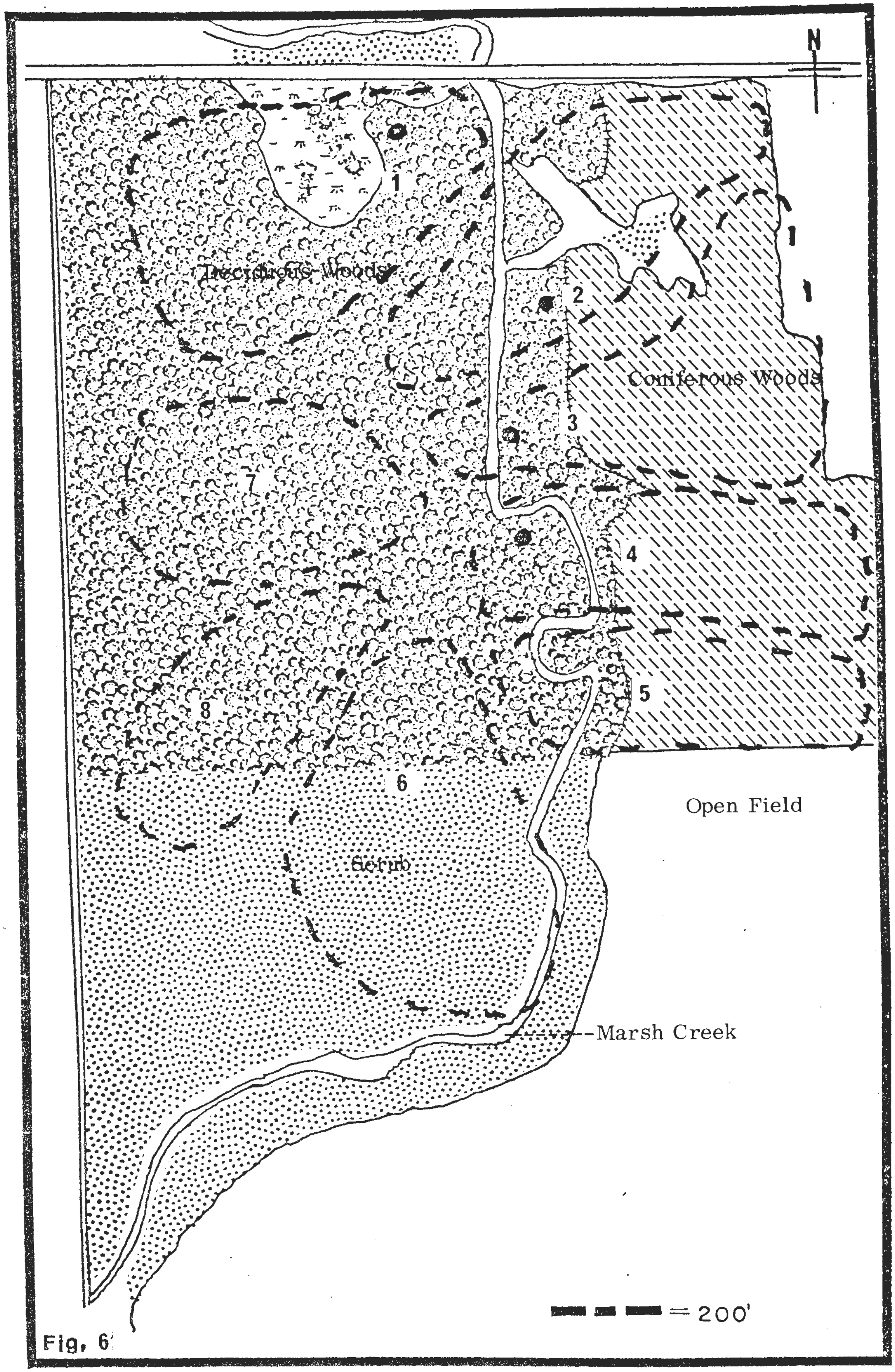

N
1
2
3
4
5
6
7
8
Deciduous Woods
Coniferous Woods
Open Field
Scrub
Marsh Creek
= 200'

Fig. 6

Figure 7. Dispersion of chickadee territories and nesting sites during the 1969 breeding season.

The dashed lines enclose the approximate boundaries of the territories chickadee pairs held.

The number identifies the pair nesting on the territory (see Figure 2). The large black dot, indicates nest located.

Legend for vegetation as in Figure 1.

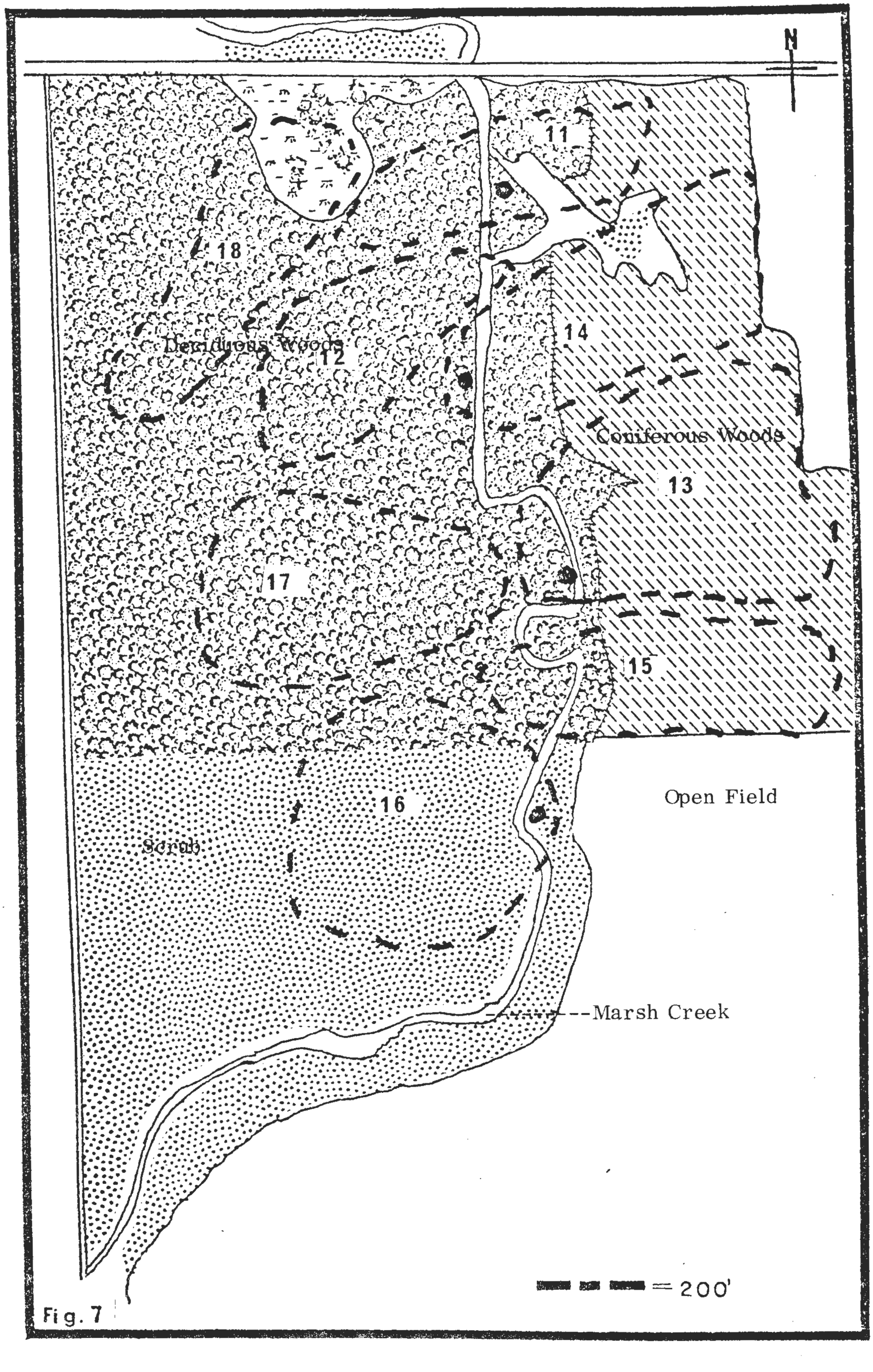

N
11
18
Deciduous Woods
12
14
Coniferous Woods
13
17
15
16
Open Field
Scrub
Marsh Creek
= 200'

Fig. 7

Figure 8. Dispersion of chickadee territories and nesting sites during the 1970 breeding season.
The dashed lines enclose the approximate boundaries of the territories chickadee pair held.
The number identifies the pair nesting on the territory (see Figure 2). The large black dot, indicates nest location.
Legend for vegetation as in Figure 1.

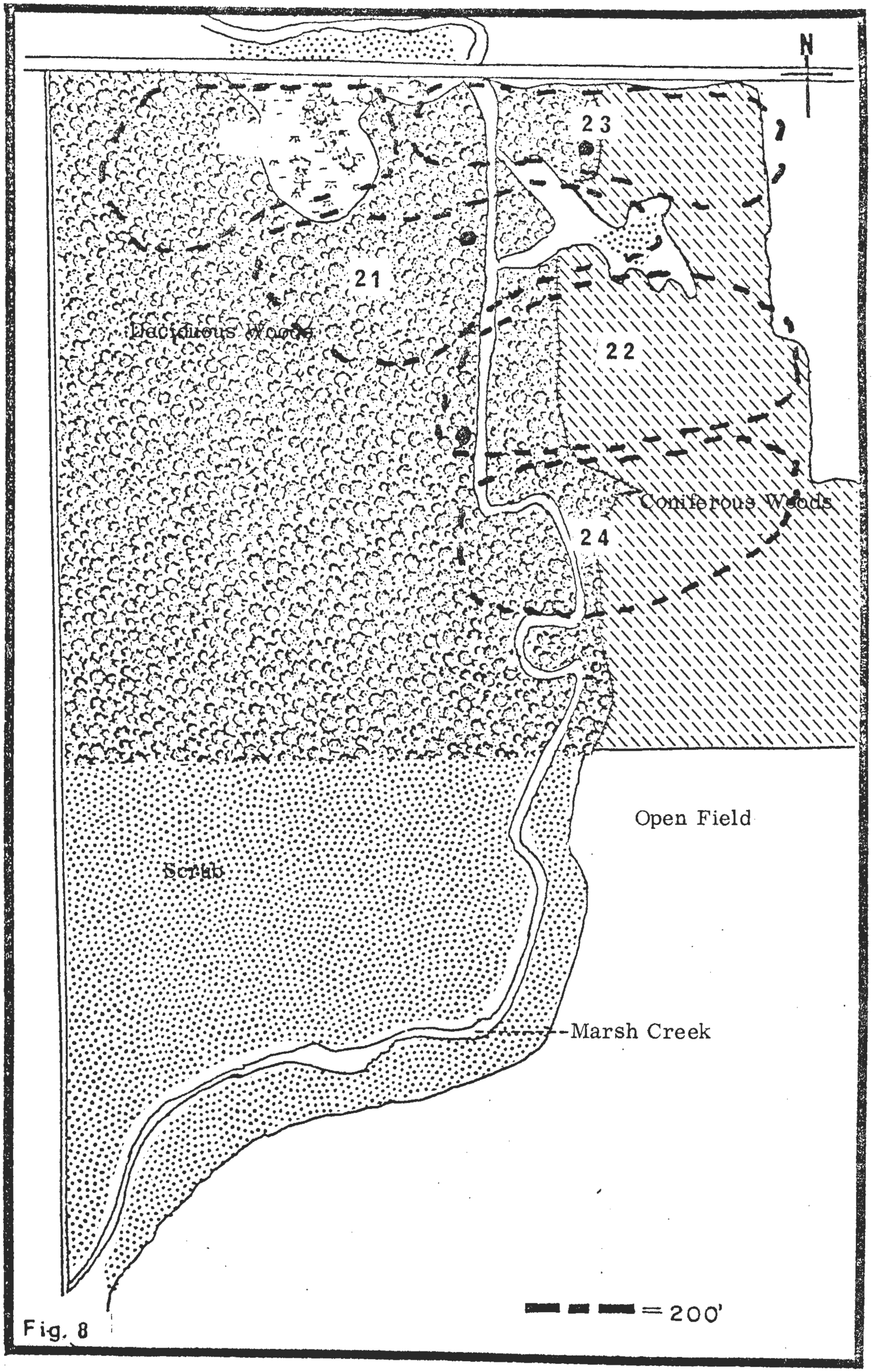

N
23
21
22
24
Deciduous Woods
Coniferous Woods
Open Field
Scrub
Marsh Creek
= 200'

Fig. 8

only breeding pair of Black-capped Chickadees that Aldrich (1943) notes in his paper were nesting in a hydrarch community.

I placed six nest boxes randomly throughout the coniferous woods in February, 1968. These boxes were left in place throughout the study. The nest boxes were never used by chickadees, apparently because of the numerous near-by dead trees available for nesting. The deer mouse (Peromyscus maniculatus) used these boxes extensively. Chickadees were never observed to attempt excavation or nesting in coniferous woods.

Fifty percent of the breeding territories on the study area included some part of the coniferous woods. The members of flocks A1, A2, and A3 included the greatest acreage of coniferous woods in their nesting territories. Mated pairs of chickadees not retaining a relatively high portion of coniferous woods in their territories seemed more likely to disappear. A comparison of Tables 4 and 5 with Figure 2 indicates that males having coniferous holdings were on the study area for a mean time of 25.5 months. Males without coniferous holdings were in evidence on the study area for an average of 17.4 months. Females whose range included the coniferous portion averaged 15.6 months on the study area, while females ranging mainly outside the coniferous woods had a mean time on the study area of 15.0 months. It was not possible to document whether disappearances from the study area were a result of high mortality, emigration or a combination of both. The relative stability of flocks A1, A2, and A3 tends to support the interpretation that the incorporation of coniferous woods in both the breeding territory and flock range is beneficial to survival.

Flock Assemblages--Their Seasonal Duration and Age Composition

Data from my field notes indicates that there were essentially four types of assemblages of Black-capped Chickadees on the study area. These were: (1) family parties consisting of the parents and their fledged offspring; (2) bands of first-year birds; (3) the winter flock of resident adults (who seem to have assembled at the time of the post-nuptial molt); (4) winter bands of first-year birds and possibly including non-resident adults.

The following details concerning flock assemblages, their seasonal duration and age composition, are presented as examples to illustrate the observations which led me to recognize distinctions among the chickadee groups on the study area.

During the 1968 post-nuptial molt, I could identify the alpha bird and his mate of flock A2 (M2 and F14), traveling with two other banded birds (whom I could not identify) as early as 25 July, 1968. As these birds completed their molt and became less retiring (approximately 12 August, 1968) I was able to identify the companions of M2 and F14, as their former winter flock mates M13 and M15. I assumed that the unidentified, banded birds seen with M2 and F14 in July were M13 and F15. Subsequent observations indicated that these birds remained together (with the exception of F15 who disappeared 15 October, 1968) as the 1968-69 winter flock (note changes to A2, A3 , see Figure 2). It would seem that resident birds' winter flocks first form as molting flocks (in a restricted range, Figure 11) and progressively become more cohesive during the winter months. However, my observations of such flocks were not extensive enough during post-molting (late summer to early autumn) to attest to the cohesiveness of such assemblages. Therefore I recorded only the cohesive winter flock in Figure 2.

The molting adults of flocks A3 and E that had survived from prebreeding season winter flocks re-formed on about 12 July, 1969 (11 days earlier than A3 was observed in 1968). The range of the molting flocks was not the same as their preceding winter range (Figure 11). While undergoing the post-nuptial molt, these birds were quiet, secretive and relatively restricted in their movements. The adults left the territory, and as Stefanski (1967, 265) also observed ". . . frequented areas with dense undergrowth . . . ." Continued observations throughout the season confirmed that the members of flock A3 and E continued through the winter as cohesive flocks until the commencement of territorial activities in April, 1970.

It is known that the family parties (of at least M2 and M13) were still intact on 4 July, 1969. This is evidenced by an altercation which occurred on 4 July, 1969 between M2 and M13, as they, with broods "in tow", crossed paths while foraging in the coniferous woodland. After this date, several significant observations were made:

Banded young of mixed parentage were observed traveling together in bands 8 July 1969; no adults in evidence (membership in these bands was not stable enough to merit assignment of a letter designation);
Four adult birds of antecedent winter flock A3, were observed together without young 12 July 1969;
Four adult birds remaining together to form winter flock E were sighted 12 July 1969, without young.

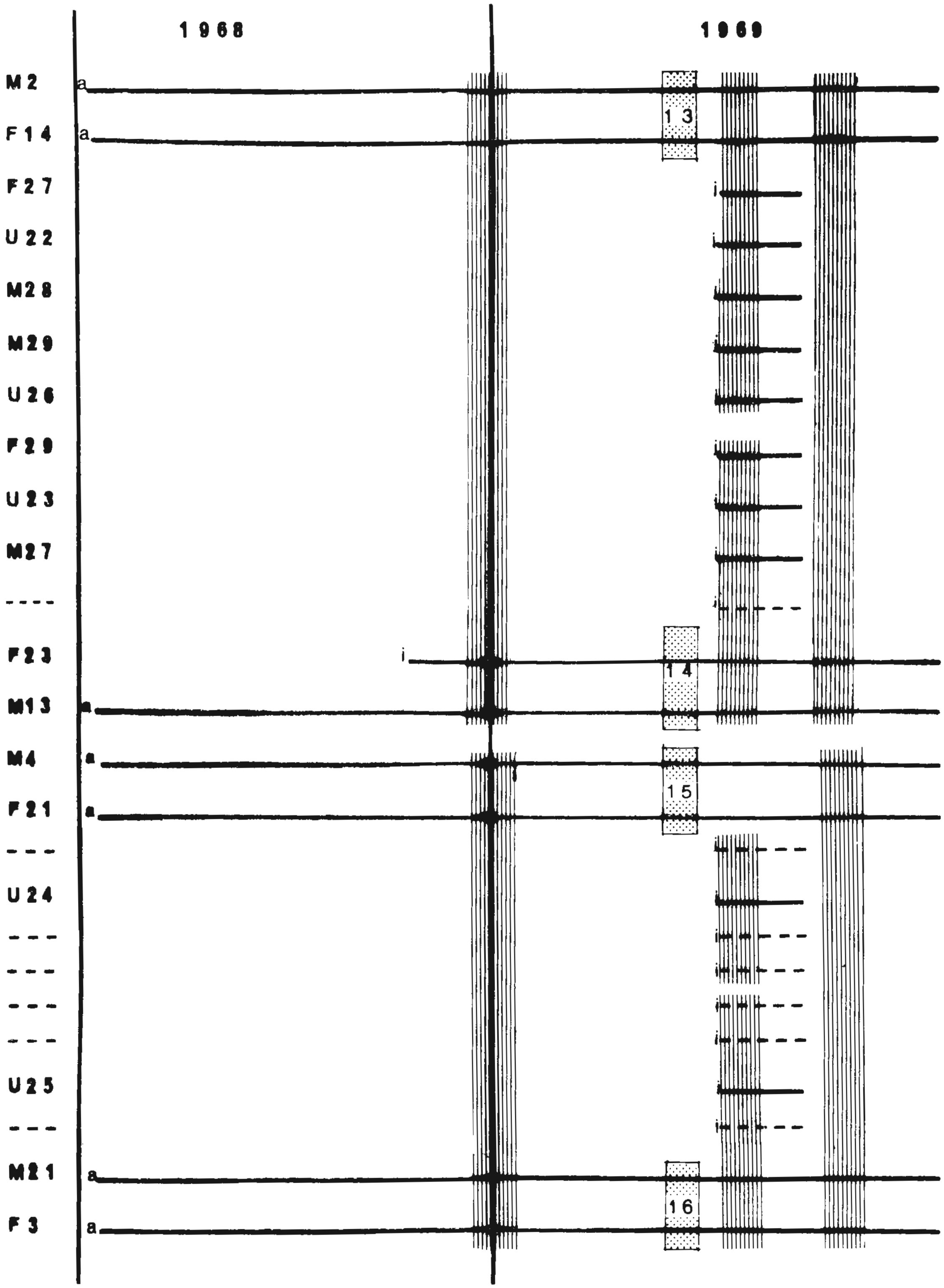
Therefore, the shift from family group to flock organization (in 1969) occurred sometime between 5 July and 8 July, 1969. From examining this evidence, it appears that the formation of post-breeding flocks composed of adult birds is deferred until the young are independent.

Some winter flocks consisted only of adults, some only of first-year birds, and others included both age groups. Adults were joined by one first-year bird after the disappearance of an adult member (flocks A1, and C1, Figure 2). There were two cases, 25 March, 1969 and 3 April, 1969, when a known first-year bird temporarily attached itself as a subordinate to a winter flock (flocks E and F) of adult birds which had an even number and a 1:1 sex ratio. One individual, (U20), remained with flock F until 10 April, 1969 (17 days) after which time it was never seen again. Another first-year bird (U21), attached itself as a subordinate individual to flock E (for 15 days) about 3 April, 1969, subsequently vanishing about 18 April, 1969. The reverse of this pattern, i.e., adults joining a flock of first-year birds was not observed. When Odum (1942, 501) commented ". . . a given chickadee flock may contain a relatively stable element,--the local adults--and/or a relatively unstable element, the first-year birds," he described well the situation which I observed.

From these data it seems reasonable to conclude that first-year birds function as replacement for missing members of established flocks (composed mainly of adult birds). First-year birds not finding a place among the established flocks of adults, form flocks of immatures.

Age composition of flocks varied with season and circumstances. From 16 June, 1969 until 8 July, 1969 bands consisted of family parties (the mated pair and their newly fledged offspring). As the fledglings of flock A3 and E became independent and the parents commenced molting, a distinct shift in flock composition occurred (Figure 9). The immatures formed two flocks. Success in prior banding of fledglings while still traveling with their parents, enabled me to determine that one group was composed of some local immatures (i.e., those which I was able to band) and other immatures of whose origin I could not be certain. I considered those unbanded individuals as immatures because of the juvenile appearance of their plumage, their association with known immatures and the fact that mature, banded adults were secretive while experiencing the post-nuptial molt at this time. The two rather loosely organized bands of immatures wandered indiscriminately over the study area. However, they were most frequently observed in the ranges indicated in Figure 10.

Figure 9. Flock composition of Black-capped Chickadees post-fledgling flock 16 June to 8 July, 1969: molting and winter flocks 12 July, 1969, through winter 1970. Horizontal bars indicate tenure of marked individuals; rows of dashes that of unmarked birds. Rectangles with background of vertical lines enclose the bars representing members of given flock during the time interval charted; numbers in rectangles show breeding pairs with territory number (Figure 2).


1968
1969
M2
F14
F27
U22
M28
M29
U26
F29
U23
M27

F23
M13
M4
F21

U24

U25

M21
F3
a
i
13
14
15
16

Fig. 9

Figure 10. The post fledgling ranges of two bands of first-year birds 8 July through 4 August, 1969 are enclosed by the solid lines.

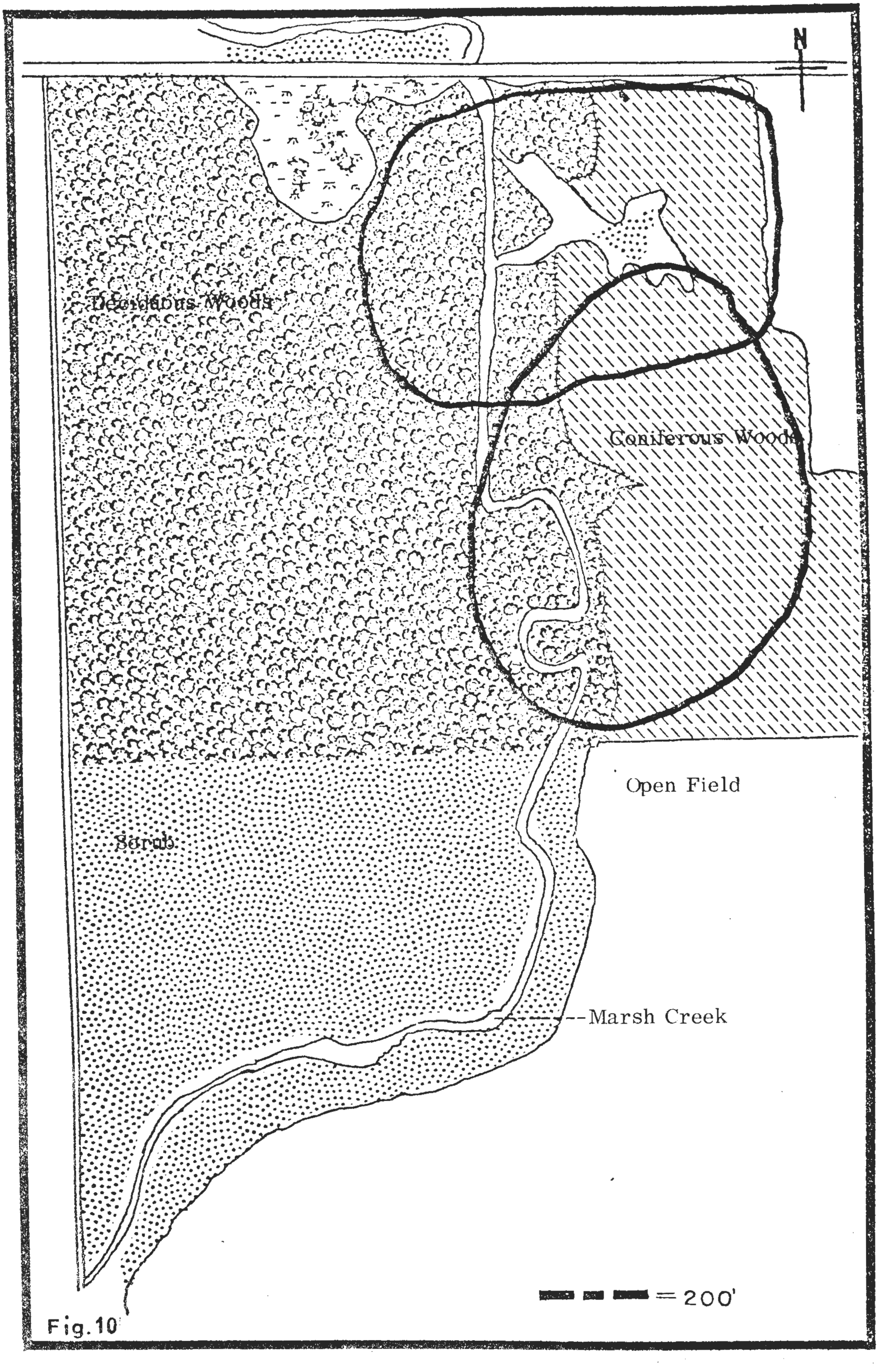

N
Deciduous Woods
Coniferous Woods
Open Field
Scrub
Marsh Creek
= 200'

Fig. 10

Figure 11. Ranges of molting adults (July-August, 1969) compared to the winter range of the same flocks (November, 1968-March, 1969). Upper case letter designate the flock. Lower case letters m, indicate flock range during molting. Lower case w, indicates pre-breeding season winter flock range. Solid line encloses molting range, dashed line encloses winter range.

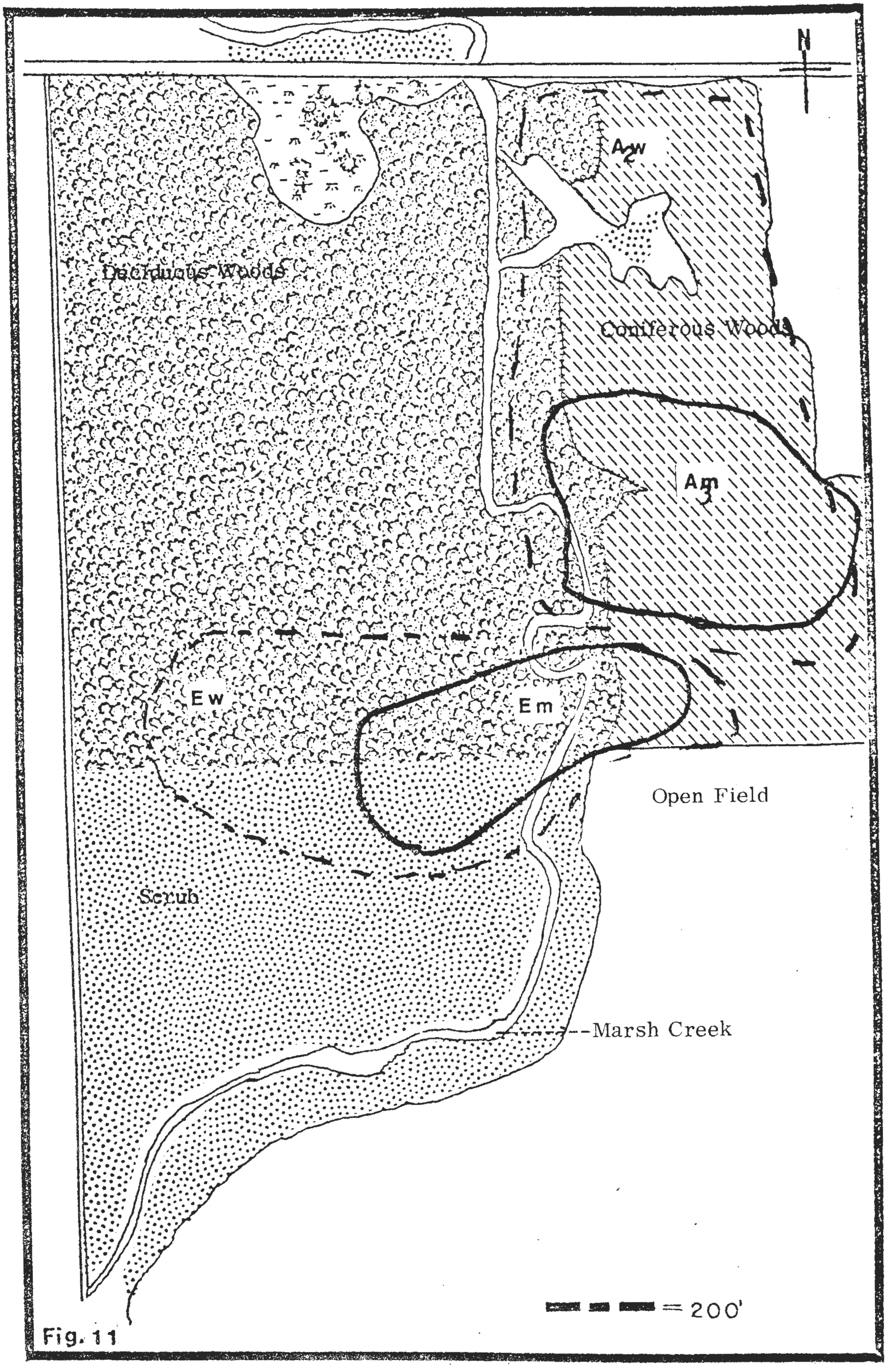

N
A2w
Deciduous Woods
Coniferous Woods
Am3
Ew
Em
Open Field
Scrub
Marsh Creek
= 200'

Fig. 11

DISCUSSION

Dixon and Gilbert (1964, 63) stated ". . . that adult Mountain Chickadees are sedentary on their breeding grounds, and that in winter months they form stable social groups in which the sexes are approximately equal." The resident flocks of Black-capped Chickadees in this study were also sedentary on a range that often included part of their breeding grounds, formed stable social groups, and for the most part maintained an even sex ratio. This is especially illustrated by resident flocks A1, A3 and C1. These flocks were composed of individuals which were assoicated as bisexual pairs and mated in the subsequent breeding season. Free floating flocks (composed mainly of banded first-year birds which were seen and recognized from time to time in the area), and itinerant flocks (unbanded birds supposedly passing through the area) were prone to having uneven sex ratios (as determined by the Mosher-Lane Method). The only three resident flock members which disappeared were replaced from the free floating population. Southern and Morley (1950), from their studies of the Marsh Tit (Parus palustris), stated that in winter there is, in addition to territory holders, a free floating population of birds unattached to territories. Mate replacement for territory holders of that species comes from the free floating population, often the next day after a territory holder's loss. In some cases such replacement took from 3 to 6 weeks, although, Morley believed this to be an unusually long time. My findings on the Black-capped Chickadee on the study area seem similar to the reports of Southern and Morely, in that groups of birds not having established themselves as resident flocks, function as a reservoir for mate replacement in resident flocks. This would seem to at least partially explain why resident flocks tend to have an even sex ratio and flocks of first-year birds tend to have an uneven sex ratio. Group size of 3 and 5 were noted among first-year birds, reflecting the uneven sex ratio.

This observation also raises the question of pairing among first-year birds. Morley (1950) stated that she did not know at what age the juvenile mates in Parus palustris paired. Hinde (1952, 42), in referring to P. palustris, stated

> In June some individuals of a color-ringed brood were seen by both J. A. Gibb and the writer to keep in pairs with other unmarked juveniles for several successive days after the break-up of the broods. These birds showed aggressive behavior towards other Marsh Tits in exactly the same way as paired birds in spring; but, if these were pairs, they were of only a temporary nature; a fortnight later the birds concerned had moved to a different part of the wood and were no longer apparently paired, though still showing aggressive behavior. In some cases, however, juveniles certainly became paired by November.

Similarly, Dixon (1949) suggested that in P. inornatus (the Plain Tit) the juveniles become paired soon after the break-up of family parties. While studying the Great Tit (Parus major), Krebs (1971) found when territory holders from the wood were removed, replacement came mainly from paired first-year birds which had held territories in hedgerows. If the first-year Black-capped Chickadees in my study area had been paired, replacement would have been by pairs rather than by individuals, as Krebs observed.

Further, if criteria such as feeding privilege, equal sex ratio in a flock, and an obvious preference of individuals in a flock for each other's company, are considered to be evidence of pair formation, then the data gathered in this study do not support pairing of first-year Black-capped Chickadees with each other until just prior to the breeding season. Flocks of known first-year birds were not observed to demonstrate these attributes. These criteria were readily observable in resident flocks composed mainly of birds which had experienced one or more breeding seasons.

Although there was no indication of pairing among individuals comprising bands of first-year birds from the time that the family parties broke up in July until nesting season the next May, there did seem to be individual recognition. This is evidenced by the hierarchy observed in two bands of first-year birds (H and I). Other than the dominance hierarchy no special relationship could be detected between male and female members of these bands during the mid-winter flocking period. There was a tendency toward polarization, with males often foraging at some distance from the females of the first-year groups. This was observed often in flock H.

Another point concerning the pair bond is pertinent here. Hamerstrom (1942) commented on not noticing any indication of a strong pair bond among the birds she was observing at her feeder. It is possible that the majority of birds she was watching could have been first-year birds, making up free-floating flocks. If indeed this was the case then one would not expect to find signs of pairing. Wallace (1941) noticed the tendency of certain individuals to stick together. The flocks he was observing could have been made up primarily of birds having experienced one or more breeding seasons, thus having formed a strong pair bond.

Morely (1950, 387) stated "No known male or female Marsh-Tit was recorded forming a pair without also claiming territory or being in residence in one, ..." Perhaps this behavior of the Marsh Tit gives insight into the pairing of first-year Black-capped Chickadees with each other. The first-year birds are not known to hold territories until the breeding season. The act of choosing and defending a territory by two birds may be an important aspect of pairing and formation of the pair bond. It appears that after having experienced one nesting season the pair bond is rather well established. Therefore, if claiming a territory is a vital aspect of establishing pair bonds it is understandable that birds never having had the opportunity to establish a territory would not be able to form the strong paid bonds observed in the resident adults. However, this does not eliminate the possibility of strong associations being developed between males and females in bands of first-year birds. This speculation that the territory plays an important part in cementing the pair bond which may be the reason that first-year Black-capped Chickadees do not seem to illustrate a pair bond until they have been through a nesting season together, does not agree with Odum's observations. Odum (1941, 317) stated "In the chickadee, however, my observations indicate that sexual bond is formed before and usually not in connection with the establishment of nesting territory which is defended later."

However, Odum (1941, 319) stated ". . . there was little evidence to indicate a mated condition prior to the time the pair actually separated out from the flock in the spring." It seems to me that again there is confusion in reporting behavior of Black-capped Chickadees, because the behavior of first-year birds is not being recognized as varying from that of resident adult birds. Obviously more field work must be done, keeping in mind that the behavior of first-year individuals and groups of these individuals can vary from the behavior of adult individuals and resident flocks of adults.

Tenure of individual birds on the area from the time of initial banding until termination of this study averaged 15.2 months for males and 14.3 months for the females. The male observed longest on the area (M2, alpha of flock A3) was present for 31 months and still living at the termination of the study. The female known longest on the area (F14, the mate of M2) had been there 30 months and was still living at the end of the study. These tenures are similar to those cited for the Marsh Tit by Southern and Morely (1950) and those cited by Dixon (1963) for the Carolina Chickadee. However, Dixon's work dates from the individual's first March rather than from banding.

It is interesting to note that the longest tenured birds were members of flocks A1, A2 and A3. These flocks held a winter range mainly in conifers, and flock members included the largest portion of conifers in their breeding territories (Figures 3, 4, 5, 6, 7, 8). One might reasonably expect birds to live longer having the advantage of dense evergreen cover, because of the protection available from predators and harsh weather.

Flocking at times other than the breeding season has been noted by numerous workers, and much speculation has been offered to explain the reason for it. Winterbottom (1949) and Rand (1954) were not enthusiastic supporters of the idea that flocking has considerable protective value. However, many, including Miller (1922), Hindwood (1937), Allee (1938), and more recently Short (1961), believe that flocking is of great value to the individual. Short stated that the advantages of foraging flocks are increased in the number of receptor systems to detect predators and mutual aid in locating food. Allee (1938) commented on the confusing effect the flock has on predators and the distraction it offers them. It seems reasonable to speculate that a particular area has its own selective pressures on the flock size of birds habitually using it; therefore, size and behavior of the flock, as well as behavior of individual birds, might vary in concert with that particular physical and biological environment.

For a migratory or roving flock of birds, continually crossing unfamiliar country, it seems that a relatively large flock would be of greater advantage than a small flock. The larger flock would multiply the advantages of flocking cited by Short and Allee, and thus promote relatively higher survival among such flock members. Perhaps this explains one of the reasons why the largest flocks of Black-capped Chickadees sighted have apparently been migrating. A large flock would not be of advantage on a restricted area, such as that occupied by the resident flocks of this study. Familiarity of territory by small resident flocks would tend to compensate for fewer receptor systems in predator avoidance and food detection. Indeed, a large resident flock of 50 or more birds on a 40-acre woodland would tend to over use the environment and eventually affect its carrying capacity. In addition to factors such as restricted range and limited resources an element of tolerance of its own kind may have precluded resident flock densities higher than four birds, by providing a form of population control outside the breeding season. Lehmann (1953) found such a factor influencing bobwhite quail densities during the winter in southern Texas.

Resident flock size limitation and predictable spatial and temporal routines of each resident flock implies a stability within the "bird community." Such stability confers order, this in turn tends to promote longevity, rather than a disorderly unstable situation whose members could be more subject to exposure and predation.

The direct effect of the physical and biological environment on flocking can, to some degree, be detected throughout the annual cycle of the Black-capped Chickadee. The mid- to late-summer portion of this cycle can be instructive in this vein. At the time of the break-up of family parties, the first-year birds tended to form relatively large bands having no apparent stable organization. Membership and size of the band seemed to shift considerably the first few weeks after the break-up of family parties with these flocks ranging over a great portion of the study area. At the same time the parents of some of these birds were undergoing the post-nuptial molt, being very quiet, secretive, and restricting themselves to a limited area of dense vegetation. The flocks of first-year birds could be large because of the obvious abundance of food at that time of year and the fact that they ranged widely over the study area, seemingly without interference from the molting adults. Even though every individual of the flock might not have been familiar with the entire area, the advantage of flocking offered them some security. As summer moved to autumn, the evidence of presumed environmental resistance and emigration was that the number of first-year birds present on the area dwindled. It is not known how greatly the ranging population of first-year birds was affected by the resumption of normal activity by the adults, following completion of the post-nuptial molt.

Since the molting adults are familiar with the area and have an abundance of food during this time, it is understandable how, under such conditions, birds could remain in a very restricted area and indeed be safe from predators. Certainly under these conditions, a large flock and much activity would be of no advantage. Thus with fair weather and abundant food the birds are able to carry on nesting and variations of flocking activities which would seem detrimental to the species during the late autumn, winter, and very early spring seasons. Therefore, time of year, local environmental conditions, age of individuals, and whether the flock is resident or migratory must all be taken into consideration when attempting to understand flock behavior.

Role of the Alpha Bird

In a resident flock the role of the alpha seems to consist of a certain amount of leadership and stabilization. The degree to which the alpha male actually exerts leadership in the flock is difficult to ascertain. It was my general impression that the alpha male was the most active bird in his flock. His activity certainly attracted the attention of other flock members and this could explain the tendency of other members of the flock to follow him. However, compulsive following of the alpha male was not observed. The pattern of following the alpha male did not seem to be regimented nor was it always continuous. At times the subordinate male and his mate might be in the lead while the flock was foraging, but the position would be changed frequently. It was most common to observe the alpha male and his mate at the head of the foraging flock. Flock stability seemed to derive from the linear hierarchy with each flock member accepting the position of the alpha and his own place in the flock hierarchy. Aspects of flock stability are discussed further on page 81.

Removal of the alpha bird for a time not exceeding 2 days had some effect on the flock. The effects on the flocks observed in the short period of removal varied slightly. Although initially, there was confusion and searching for the missing alpha bird, when next seen the birds retained a hierarchy in two of those cases with the beta male becoming the dominant bird. The temporal pattern was disrupted and flock routine somewhat changed. There was no evidence that the removal of the alpha bird had a crippling effect on the flock and it is not known whether or not such a "leaderless" flock could be easily displaced or excluded from a feeder. Lack of extensive sightings, and the relatively short period of alpha's removal did not facilitate itself understanding the impact this experience may have had on the resident flock. No permanent change in hierarchy occurred. When the alpha bird was restored to the area he resumed his former dominant role in the flock. Unfortunately time didnot permit the removal of other members of the flocks, each in their turn. Therefore it is not known if the calling, the apparent searching and the deviation in temporal feeding pattern would have been repeated had any other resident flock member been removed.

Removal of the alpha male from each of the confined flocks produced similar immediate behavior. There was much calling and activity by those remaining in the aviary. However, in a short time (about 10 or 15 minutes) the birds seemed to resume their normal aviary activity.

Artificial Feeding

Because of the relative isolation of the study area, resident flocks of chickadees were not known to have been exposed to artificial feeding. At the beginning of the study these birds did not utilize bait which had been placed at trapping stations. It took approximately two and one-half months before the chickadees on the study area responded to any form of food used as bait. In late November, response to walnut meats, sunflower seed and suet was noted. This response corresponded to the colder weather and the decrease in insect food. However, the following year, after a tradition of artificial feeding had been established, chickadees on the area readily responded throughout the year to artificial feeding, with the exception of the period of nesting, fledging and molting (i.e., late April to late August) when there was a notable lack of interest in food artifically provided.

Before the birds developed the custom of utilizing artificially occurring food, no more than four birds were observed in a resident flock. It is my contention that Black-capped Chickadees frequenting areas where feeders have been established, may tend to form larger, less cohesive winter flocks which break-up readily and re-form just as easily as a result of abundance of food. Odum (1942) commented on the considerable flexibility in flock numbers, noting how variable they could be from day to day or hour to hour. Odum's study area included a village where many inhabitants provided winter feed for the birds. Could this concentrated food source have been at least partially responsible for the variation in the numbers of individuals in the flocks he observed? Perhaps Odum, when observing small flocks which tended to stick together, was observing a resident flock, and when observing a relatively large flock, was observing a flock taking advantage of the concentrated food supply.

Other species of birds are known to form rather large flocks when taking advantage of a concentrated food source (e.g., gulls attracted to schools of fish). It seems that feeders would tend to attract roving flocks of first-year and other birds not holding residence in the area of the feeder, as well as the resident flock. This was noticed by Lawrence (1958, 418) while maintaining a feeding-trapping operation. She stated that chickadees ". . . traveled great distances to reach Pimisi Bay to winter . . . ." The attraction of roving flocks to a feeder could explain conflicting observations concerning the strength of the pair bond of the Black-capped Chickadee in winter months. Those observing flocks of Black-capped Chickadees at a feeder and noting no evidence of male-female recongition which could be considered male recognition, could be watching mainly first-year birds and/or widows or widowers, not a resident flock. Those observers recording evidence in support of a strong pair bond could be encountering mainly resident flocks. This is close to the observations made on this study area in western New York. Even-numbered resident flocks were noted before feeder installation. After installation, there was an influx of unbanded birds, some of which proved to be local birds (but not residents of the winter range including the feeder) as well as roving flocks and itinerants. As noted in the results section, the behavior of first-year birds is different from that of resident birds having survived a breeding season and still in association with their mate. These resident pairs making up the local winter flocks vary in behavior patterns depending on where they are observed. They may be observed in a congregation at a feeder on the winter range of another flock, or as a small, rather cohesive flock when foraging on their own winter range, in each case demonstrating a slightly different flock behavior pattern. As well might be expected, the behavior of an individual or a flock can vary according to the set of circumstances in which it finds itself. In comparing before-feeder to after-feeder installation behavior in this study area, a change in behavior patterns of the birds using the area was noted. There is no question in my mind that learning to utilize these various sources of artificially provided food had taken place among the original residents of the area and this information was communicated to other chickadees entering the area. Upon returning to this area after being abroad for a year (therefore no food artificially provided during my absence) I was unable to detect any banded birds. Yet when I hung walnuts at old trapping stations and put sunflower seeds in the seed dispensing feeders, they were readily used (from September on) by the unbanded birds of the area. This observation tends to support the speculation that information has been passed on from past residents to chickadees now in the area.

Site Related Dominance

There was no evidence in the data which I gathered which suggested site-related dominance, such as that commented upon by Colquhoun (1942) in the Blue Tit (Parus caeruleus); Brian (1949) in the Great Tit (P. major) and Brown (1963) in the Steller Jay (Cyanocitta stelleri). That is, I did not find that the outcome of an encounter between two individuals in the same resident flock differed according to the location of former nesting territories of the participants. There was no indication of a reversal in ranking among resident flock members throughout the flock's winter range. Similar findings were reported for the Black-capped Chickadee by Hartzler (1970) Carolina

Chickadee by Dixon (1963) and Mountain Chickadee by Minock (1971). My observations indicate that peck-right dominance in flocks of Black-capped Chickadees in this study, is retained in captivity as well as in nature.

It appears to me that learning, reinforced by duration of time, is the primary factor in retention of the flock hierarchy in Black-capped Chickadees. Crook and Butterfield (1968, 382), in their hormone experiments on Quelea, suggested that learning played a more lasting role in changes in social hierarchy than hormone injections. They stated:

> When the social hierarchy based on individual distance encounters was re-examined following the withdrawal of both injections and materials it was found not to associate with that present prior to injections. The changes suggest that during competition for materials some learning may have occurred that tended to perpetuate the changes in social status.

Social status did not change perceptibly in the three flocks studied in the aviary. Individual members seemed to hold the same social position in captivity as they had held in the wild. Even when injected with androgens the subordinate males in flocks A3 and D, did not rise in the hierarchy of these flocks. However, confusion did seem to result in flock D. A statistically significant increase in inter-individual interactions occurred, but the alpha male did not appear to lose his status nor did the injected subordinate rise to the dominant position. It is difficult to interpret such a significant increase in encounters occurring among members of flock D but not occurring among members of flock A3. One explanation is learning. Flock D was thought to have been assembled a relatively short time before their confinement and subjection to experimentation. Therefore these birds had supposedly not lived under the domination of the alpha male for very long, and the social position of each individual was not of long standing. Perhaps this contributed to the confusion which occurred when the subordinate male was injected with testosterone propionate and subsequently changed some of his former behavior patterns.

Unlike flock D, two members of flock A3 (F14, mate of the alpha male and M13, the subordinate male), were known to have held their current positions in the hierarchy under M2 (the alpha bird) for two winters and were well into their third winter season together when captured and placed in the aviary. I suggest that the positions of the birds in flock A3 were of such long standing and so well learned that the androgen injections of the subordinate male did not significantly affect the flock hierarchy nor the interactions between flock members (which in fact is supported by the data in Table 10). From this, one might conclude that learning plays a very important, if not the most important role in retention of flock hierarchy in the Black-capped Chickadees of this study. This information would also tend to explain why resident flocks of relatively long standing (with established spatial routines) were stable, while newly formed flocks of first-year birds, itinerant flocks, and migratory flocks are not stable and can readily break-up and re-form.

Positions in a social hierarchy of long standing which are well established by learning seem to be much more difficult to influence, than a position held for only a short time. Table 11 shows a statistically significant difference between flock A3 and D which suggests that this difference is at least partly due to the variation in length of time the members of these flocks had been together as a flock. This resistance to outside influence seems to underline the importance of learning as a factor in the retention of position in the social hierarchy.

In nature, a freshly filled feeder would be exploited extensively by chickadees within the first few hours of filling. Observing the birds so employed left one with the impression that they had voracious appetites and the ability to extract the sunflower seed from the seed coat at an amazing rate. The numerous trips each bird would make to the feeder left the observer wondering where these small creatures were putting the seeds. What was happening was not clear, but it did seem almost impossible that the birds could eat as many seeds as they had taken. Confinement of chickadees in the aviary facilitated observations of the birds' feeding patterns, and gave insight into the mystery of the disappearing seeds. They were being rapidly cached in various cracks and crevices in branches, pine cones, etc. This food storing and feeding behavior of the Black-capped Chickadee which was observed in the aviary and later in the field was similar to that for the Willow Tit (Parus montanus) which Haftorn (1956) observed in Norway.

Establishment of breeding territories in the area seemed to follow temporal and behavioral patterns recorded by Odum (1942) and others who have studied the Black-capped Chickadee at similar latitudes. The territory size is well within the averages for Black-capped Chickadees which Brewer (1963) has summarized. An interesting observation was the heavy concentration of nest sites and presumed nest sites in the vicinity of the creek and the area which occasionally flooded. There seem to be at least three reasons for this type of nest location: (1) the apparent preference of the Black-capped Chickadee to nest in a hydrarch community (Aldrich, 1943); (2) the abundance of dead trees providing soft wood for excavation and (3) the proximity of this area to the beginning of the coniferous plantation. Such a nest site provides easy access to the variety of food and cover which such vegetation might offer. The coniferous woodland seemed to be a favorite foraging place for the family parties after the young had fledged. In an attempt to discover if the chickadees were nesting in deciduous wood because nesting sites were not readily available in the coniferous woods, nesting boxes were placed in the coniferous woods at random locations and at a variety of heights. The boxes were not utilized by chickadees in any of the three nesting seasons. The data indicate that a higher survival rate was enjoyed by resident flocks utilizing coniferous woods during nesting season. Therefore I conclude that a coniferous woods is of advantage to individual Black-capped Chickadee survival, but plays a minor role if any in providing a nesting location.

SUMMARY

The study was conducted on a relatively isolated 40-acre woodland in western New York. The tract consisted of an 11-acre planting of 30 year old conifers and a 29-acre section of climax deciduous woods. Studies of confined flocks were carried on in an aviary at State University of New York, College at Brockport, New York.

During the period from December, 1967, to June, 1970, 33 color-banded Black-capped Chickadees (*Parus atricapillus*) were studied. A total of 12 flocks was observed from January, 1968, to March, 1970. Observations revealed subtle differences in male and female bibs and caps, which facilitated sexing of the birds. Resident flocks usually had a 1:1 sex ratio. In early spring, 1969, two instances were recorded of a first-year bird attaching itself to two resident flocks (E and F) for 15 and 17 days, respectively. In two bands of first-year birds an uneven sex ratio was recorded. It was possible to observe the members of 7 of the 12 flocks into the nesting season. All members mated with flock mates. Therefore it appears that resident flocks are usually composed of pairs.

Differences in the life style between members of resident first-year flocks was more striking than noted by earlier workers who did not distinquish age groups.

Each of the 10 resident flocks exhibited a linear hierarchy. Two flocks of first-year birds also had a linear hierarchy by January of their first-year. The alpha male's mate took precedence over other flock members at a restricted food source, but, in the absence of her mate, she usually deferred to the beta male. In one flock the alpha male's mate retained precedence at a restricted food source in the absence of her mate. In two flocks of immatures there did not appear to be pairing or any special relationship between the male and female members during mid-winter flocking. Resident flock C2 disbanded sometime during late January or early February, 1969. Subsequently the former alpha male (M23) of C2 became beta of flock E. The former beta male (M1) of flock C2 became alpha of flock F.

The residents with the longest tenure were members of a flock which included the largest portion of coniferous woods in their winter range. The alpha male of this flock was the oldest known resident of the study area. These same birds included the largest acreage of coniferous woods in their nesting territories. Male Black-capped Chickadees having coniferous holdings were on the study area for a mean time of 25.5 months. Males without coniferous holdings were in evidence on the study area for an average of 17.4 months. Females including the coniferous portion of their range averaged 15.6 months on the area, and females ranging mainly outside the coniferous woods averaged 15.0 months on the area. The common flock size of resident birds was four. Flocks of first-year birds seem to function as a reservoir for replacing lost members of resident flocks. Mate replacement in three resident flocks took an average of 14 days, ranging from 2 days to 35 days. Break-up of family parties in 1969 took place between 5 July and 8 July, and the formation of post-breeding flocks composed of adult birds was deferred until the young were independent. Evidence of flocking of first-year birds was noted at this time.

Removal of the alpha male for a period not exceeding two days seemed to affect temporal patterns in one flock. No profound effect on the flock resulting from the absence of the alpha male could be detected. The alpha male in each confined flock was removed for two hours. The remaining flock members hopped about giving the "chickadee dee" call.

Establishment of feeders affected patterns of flock size and behavior.

Each of three flocks confined in the aviary showed no change in hierarchy from that observed for that flock in the wild. The subordinate male bird received three injections of testosterone propionate. No apparent elevation in his social position was observed. In one flock an increase in encounters among members was noted, as well as greater activity in the injected bird.

Caching of surplus food was noted both in the wild and in captivity. The subordinate birds utilized the cache of the dominant birds.

The 21 breeding territories located ranged from 3.5 acres to 4.1 acres. Fifty percent of the breeding territories on the study area included some part of the coniferous woods. The average territory size in the coniferous woods during the nest building stage was 3.0 acres, ranging from 2.3 acres to 4.1 acres. The average territory size for deciduous woods during the nest building stage was 3.4 acres ranging from 2.2 to 3.5 acres.

Nest sites were heavily concentrated in a section of dead trees near the border of the coniferous sector. Six nest boxes placed in the coniferous woods were not used by Black-capped Chickadees.

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APPENDIX

A Method of Determining the Sex of Captured Black-capped Chickadees

by

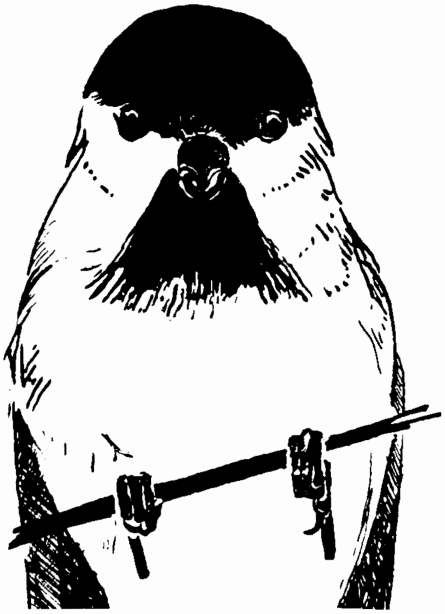
John I. Mosher and Stephen Lane

In studying the behavior and social organization of the Black-capped Chickadee (Parus atricapillus) it is important to know the sex of the birds being observed. Previous investigators have relied upon courtship behavior or the roles of the sexes in incubation; the alternative involves sacrifice of the individual for examination of the gonads.

While observing chickadees in an aviary a flash of insight led us to examine the shape and extent of the cap and bib as being subtly indicative of the sex of the individual in this species. We noted that the bibs of Black-capped Chickadees judged to be males were broader and not well defined at the posterior margin (Figure 1). The bibs of females narrow perceptibly beneath the beak, and the posterior margin is abrupt. The cap of the male is rather pointed posteriorly in contrast to the truncate margin in the female (Figure 2). The tentative designations of the sexes in captives were subsequently confirmed by observations of their behavior.

This visual comparison method of sex determination was confirmed by the examination of 21 study skins for which sex was indicated on the label.

Figure 12. A comparison of the bib of the male (left) with that of the female (right) Black-capped Chickadee.



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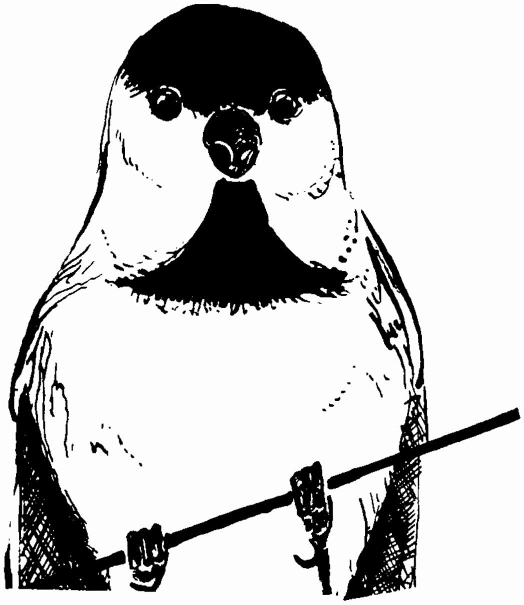

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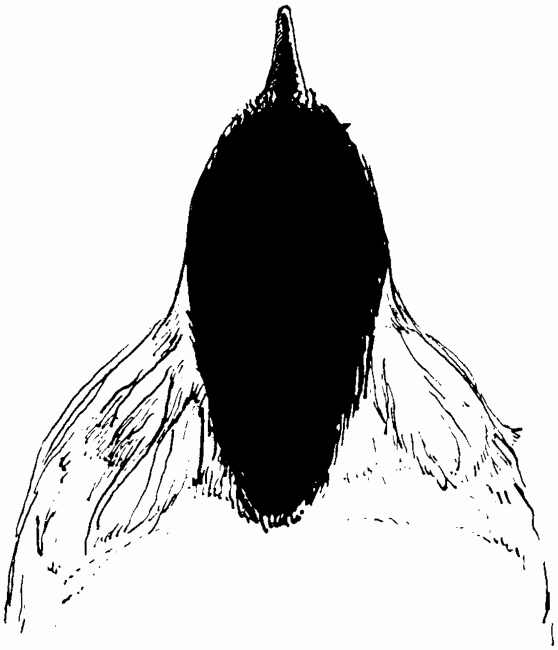
Figure 13. A comparison of the cap of the male (left) with that of the female (right) Black-capped Chickadee.



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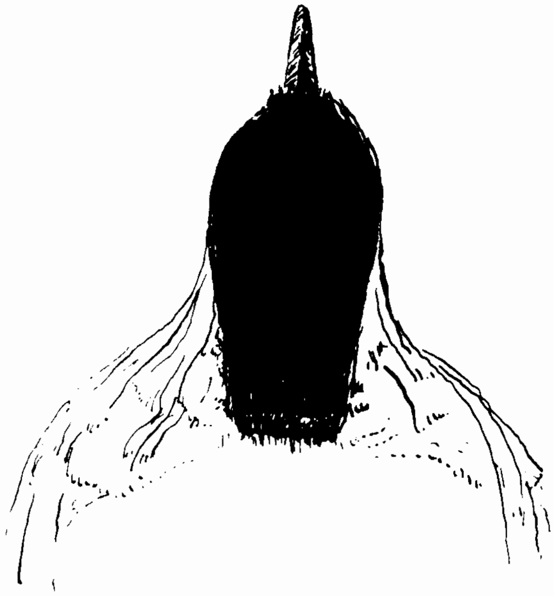

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We achieved 100 percent accuracy in our predictions, and extended this method to determination of the sexes in 20 specimens of the Mountain Chickadee (*Parus gambeli*) at Utah State University. Twelve study skins of the Marsh Tit (*Parus palustris*), and 9 of the Willow Tit (*Parus stricapillus montanis*), from a collection at the University of Manchester, England, were examined and successfully segregated by this method. However, cap configuration was the best indicator of sex on the study skins of the Marsh Tit.

With practice in observation and comparison of bib and cap configuration, a high degree of accuracy can be obtained in detecting the sex of individuals in this species (i. e. , the Black-capped Chickadee).

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VITA

John Ivan Mosher

Candidate for the Degree of

Doctor of Philosophy

Dissertation: An Analysis of Flock Organization in the Black-capped Chickadee (Parus atricapillus).

Major Field: Zoology

Biographical Information:

Personal Data: Born at Waterloo, New York, September 26, 1933, son of Ivan J. and I. May Albright Mosher; married Constance DeLong June 25, 1960; three children---Jennifer, Lisa, and John Matthew James.

Education: Attended elementary school and high school in Phelps, New York; graduated from Phelps Central School in 1951; attended post-graduate school at Waterloo High School in 1952; received the Bachelor of Arts degree from Hobart College, Geneva, New York, with a major in Psychology and minor in Anthropology, in 1956; attended United States Officers School (Navy), 1956, and U.S. Navy advanced physiology (for high altitude flying) in 1957; did graduate work at Western State College of Colorado, Harvard University, McGill University, University of Oregon, Williams College, Lyndon (Vermont) State College, State University of New York, College of Brockport; received the Master of Arts degree from Western State College of Colorado, with a major in Biology, in 1961; completed requirements for the Doctor of Philosophy degree, at Utah State University in 1972.

Professional Experience: 1958 to 1959, research assistant New York State Experimental Station Cornell University; 1959 to 1960, instructor of biology at Lyndon Institute, Vermont; 1960 to 1961, staff member biology department the University of Rochester; 1961 to 1965, assistant professor of Biology, State University of New York, College at Brockport; 1956 to

1967 (while on leave from Brockport), half-time instructor at Utah State University in Zoology; 1967 to 1970, Associate Professor State University of New York, College at Brockport; 1970 to 1971, Senior Research Fellow in Zoology at University of Manchester, England (while on sabbatical from Brockport State); September 1971 to present Associate professor in Biology at State University of New York, College at Brockport.