SEASONAL CHANGES IN THE SURVIVAL OF THE
BLACK-CAPPED CHICKADEE

by

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B.Sc., University of British Columbia, 1963

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in the Department of
ZOOLOGY

We accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA
September, 1965

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Date Sept. 10 1965

ABSTRACT

A population of Black-capped Chickadees (Parus atricapillus) living in a favourable environment was colour-banded, and its survival was followed, to find out what prevents continual increase in its numbers. A weekly census of the population was made throughout the two years of the study. All nests were found and the young were banded before they flew. Every two weeks throughout both winters checks were also made on an unbanded population in a control area one and a quarter miles from the main population.

Nesting success was high in both years, with 5.0 young per pair being fledged in 1964 and 4.5 young per pair in 1965. Juvenile survival until family break-up was almost 100% in both years; juvenile survival until September seemed to be high. The survival rate of the adults was uneven: there were two periods when it was lower than it was during the rest of the year. The less sharply defined period occurred during the post-breeding moult of the adults. The more sharply defined period of two weeks or less was exactly correlated in both years with a change in behaviour from flocking to territorial behaviour. With the exception of one unmated female in each year, every bird which survived this critical period remained to breed or attempt to breed; hence this change in behaviour in the spring evidently removed surplus birds

from the area, and thus prevented continual increase in the population. This behaviour may be the common factor that limits the breeding populations of other species with similar ecology.

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ACKNOWLEDGEMENTS

I wish to express my sincere appreciation to Dr. D. H. Chitty for his valuable advice and encouragement throughout this study. Gratitude is also expressed to Dr. P. A. Dehnel and to Dr. I. McT. Cowan for their critical reading of the manuscript.

I am very grateful to Margaret Skirrow for her help in the field and with the manuscript. The assistance of Gail O'Hagan is also greatly appreciated.

This study was aided by grants to Dr. Chitty from the National Research Council of Canada.

INTRODUCTION

This study attempts to answer the following general question: what prevents continual increase in a population whose environment is apparently favourable?

To be suitable for a study of this sort, a population must be living in an environment where losses caused by predation, disease, food shortage and other accidents are likely to be minimal, for only in such a favourable environment can surplus birds occur. Also, it must be possible to estimate the population at frequent intervals.

Because it seemed to fulfil both these requirements, I chose a population of Black-capped Chickadees (Parus atricapillus L.) living in a residential area and surrounding woods on the University Endowment Lands. The problem then reduced itself to finding out when surplus birds disappeared each year and what factors were associated with this disappearance.

The Black-capped Chickadee is a hole-nesting passerine with a fairly large clutch size (Peterson, 1961, gives a range of 4-9 eggs). It reaches maturity and breeds the first year after hatching. In North America it ranges over most of the continent: In British Columbia it is "resident throughout the Province except in the Gulf Islands, Coast Forest, Queen Charlotte Islands and the Alplands

biotic areas" (Munro and Cowan, 1947). Vancouver is thus neither the most northern nor the most southern extreme of its range, and it is a non-migratory resident in this area. Like many other members of the genus Parus, this species is strongly territorial during the breeding season, but spends the rest of the year in flocks, thus exhibiting two distinct seasonal modes of behaviour toward other members of the same species.

The project was started in 1963 with the hypothesis that the mortality rate in a favourable habitat is not constant, i.e. there are certain periods during the annual cycle when sudden drops in numbers occur. The object of the study was to investigate the causes of these sudden losses.

Although there has been much work on the population ecology of the family Paridae, there is no agreement that any one process determines the breeding density of titmice. There are apparently three main schools of thought as to what factors have the most control of the breeding density of titmice. Gibb (1954, 1956, 1960, 1963) claims that winter food shortage is the main factor determining the breeding density. Lack (1957, 1958), originally supporting Gibb's hypothesis, now agrees with Perrins (1963), who writes that in the Great Tit the survival of the young in late summer or autumn, depending on the food received earlier, seems to be the most important factor affecting the breeding density of this species. Finally, Kluyver & Tinbergen (1953)

claim that in favourable habitats the breeding density seems to be a consequence of territorial behaviour, with surplus birds going into the less favourable habitats. The latter authors are the first to suggest that surplus titmice are eliminated from favourable habitats by territorial behaviour. However they were more interested in their proposed "buffer" mechanism than in the effect of territories as such, and so did not pursue the idea that breeding density might be regulated by territorial behaviour. In each case the populations studied were at least partially migratory, which necessarily complicates the interpretation of data, and none of the observations is sufficiently detailed to rule out alternative explanations.

STUDY AREA:

The study area consisted of approximately 160 acres adjacent to the University of British Columbia campus (Figs. 1 and 2). The boundaries of the area were drawn somewhat arbitrarily, to include as many flocks as could be censused each week. The area was part of a residential area, and included strips of woods along the east and west sides. As the boundaries were chosen from flock ranges, they were in effect isolating as long as the flock structure remained intact. Beyond the east side was the campus, and beyond the south side, a large open park; both these were physically

more isolating than the other two sides. However, as inter-flock exchange of individuals in this study was extremely rare, the boundaries were considered to be quite effective.

There were many mature shade trees in the gardens throughout the residential part of the area. Nest sites in this section were in Dogwoods (Cornus nuttalli) most frequently, but a Red Alder (Alnus rubra), an old apple tree, and even a rotten fence post were used.

The woods on the east and west sides of the area were second growth and had a canopy composed of roughly 85% Red Alder, with some Dogwood, Bitter Cherry (Prunus emarginata), Cottonwood (Populus trichocarpa), and a very few Douglas Fir (Pseudotsuga menziesei) and Red Cedar (Thuja plicata). The understory was composed of Salmon-berry and Thimbleberry (Rubus spectabilis and R. parviflorus), Redberry Elder (Sambucus pubens), Salaal (Gaultheria shallon), Trailing Blackberry (Rubus vitifolius), and Broom (Cytisus scoparius). Red Alder was the only tree used as a natural nest site by chickadees in the study woods.

To make the area as favourable as possible, nest boxes were put up throughout the area and feeding stations were maintained during the winter. Thus there was always an excess of food and nesting sites.

Since it could always be argued that this population was not living under sufficiently natural conditions, control observations were made in a natural forest one and a quarter

miles from the main study area. The canopy was 55% deciduous and 45% coniferous, the major trees being Red Alder, Broad-leafed Maple (Acer macrophyllum), Douglas Fir, Western Hemlock (Tsuga heterophylla), and Red Cedar. The understorey was mainly Redberry Elder, Thimbleberry and Salmonberry. This area contained many old Alders and Maples, so there was again an excess of nest sites.

The control area was approximately the same size as the main study area, and each winter supported at least three flocks. Each flock contained 6-12 chickadees; thus when the flock break-up occurred in the spring, the difference was easily observed even though the birds were unbanded.

METHODS

a) Bands

Each marked bird was given a numbered aluminum band supplied by the Canadian Wildlife Service, and from one to three coloured split plastic bands bought from A. C. Hughes, Middlesex, England. Six colours were used: red, yellow, green, blue, orange, and black. These were distinguishable in the field; any more colours have been found in other studies to be confusing. Each individual marked in the study had a different colour combination. During both winters chickadees were captured with mist nests placed near feeding stations. This method of capture was successful only from early November to the end of February, as this is the only period when chickadees come regularly to the feeding stations. At first the young were marked at the nest at 10 to 14 days of age. Later broods were marked when they were nearer to ten days old, because it seemed that at an earlier age disturbance was less likely to make the nestlings leave the nest prematurely. In each case only part of the brood was removed at any one time to reduce the possibility of the adults' deserting the nest. No desertions occurred during the study after the young had been banded.

b) Records

Regular checks on the population were possible because the study area was adjacent to the campus. Sight records of the population were made at least once weekly throughout the project. The presence and behaviour of each marked individual were recorded, as were the locality and composition of the flock.

c) Control Observations

One whole morning's observations were made every two weeks through the winter on the control area. Estimates of the numbers and checks on the behaviour of individuals were made. However, as there were no marked birds in this area, these estimates were not as accurate as those in the main study area.

d) Nest boxes

During the study, 42 nest boxes were put up. Of these, 33 were hung in the built-up part of the study area during the first year, the remaining nine were added in the first week of March 1965 in the woods after the felling of a narrow strip of mature Alders which had had four nests

in 1964. All nest boxes were half-filled with sawdust. Other workers have found that this makes them more acceptable to chickadees (Kluijver, 1961; Drury, 1958), since this species normally excavates its own nest hole in soft wood. The boxes were placed at varying heights (most between seven and fifteen feet) and faced in varying directions; all were attached to the main trunk of a tree at least four inches in diameter.

e) Survivorship

These data are presented in the form of lx tables according to the methods described by Andrewartha and Birch (1954). As the counts were complete for banded young between the time they left the nest and family flock break-up, no special problems arose for juvenile survival. However, in the case of the adults, some individuals were missed in almost every fortnight. This introduces certain difficulties in arriving at a figure for the probability of surviving a given time interval (Chitty, 1952). Therefore lx curves for the adults were compiled from minimum survival rates based on the individual fortnightly samples.

If the minimum survival rates were much below the true rates, the annual survival rate obtained by this method would be grossly below the true figure. Therefore the data have been examined for such a bias. For example,

of 11 birds observed in the first period of the second year (1964-65), two were known to be alive almost a year later - an observed minimum survival rate of 0.18. The rate calculated from the individual samples is slightly greater than this (0.23, Table 5). Other intervals have been examined in the same fashion, and any bias that may be present appears to be concealed by errors of sampling.

RESULTS

a) Natural History

i) Establishment of Pairs. In this study all pairs were formed between members of the same flock, although Odum (1941) reported at least two instances in which pairs were formed between birds from different flocks. Whenever both members of an old pair survived the year, they remated, having stayed together all winter.

ii) Territory Formation. There was a period in the spring not exceeding two weeks in each year when the change from flocking to territorial behaviour occurred. Prior to this period, the birds were in winter flocks (Figs. 1 and 2), and were not observed fighting even when two flocks met. (Fights at feeding stations are not included here.) During this period flock members which had fed quietly together all winter were frequently seen fighting, and after this period all the chickadees remaining on the area were paired, and defended a territory (except for unmated females which were tolerated by territorial pairs). Table 1 shows the spring pattern of observed aggressive encounters in the study area in both years. An "agressive encounter" was nearly always a prolonged chase accompanied by "fighting notes" and "dominance notes" (Odum, 1942); actual contact between fighting chickadees was observed

TABLE 1.

Number of observed aggressive encounters in the spring: main study area.

Period	1964												1965																	
FF	.	.	0	.	0	0	0	0	.	0	.	1	.	1	.	0	.	.	0	.	.	0	0	0	.					
FM	.	.	3	.	1	<u>4</u>		.	.	.	.	<u>5</u>	.	<u>6</u>	.	.	0	0	.	.	0	.	0	2	.	.				
MM	.	.	.	.	.	.	.	3	.	.	2	.	.	<u>4</u>	<u>6</u>	.	<u>6</u>	.	<u>8</u>	<u>7</u>	<u>7</u>	.	<u>4</u>	.	3	2	.			
MM	.	2	.	3	.	2	.	.	2	.	0	1	.	.	3	2	1	.	1	.	1	.	2	.	.	1	.	.		
MA	.	.	.	1	.	1	1	.	1	.	.	.	1	2	.	.	0	1	.	.	1	2	.	.	.	.	1	.		
AA	.	.	.	.	1	.	2	.	.	.	.	.	1	.	2	.	.	.	1	.	.	.	1	.	0	.	.			
AM	.	.	.	.	.	.	.	0	1	0	1	1	.	1	0	1	.	.	.	0	0	.	.	.	1	.	.	1		
MM	0	.	0	0	1	1	.	0	1	0	1	1	.	0	.	.	.	0	.	.	.	0	.	.	0	.	.	0		
MJ	0	0	0	0	0	0	.	.	0	0	0	0	0	0	0	.	0	.	0	.	0	.	.	0	0	0	0	.	0	.

Note: figures in red are those above 3; this figure was chosen arbitrarily to indicate the peak of aggression in each year.

F = February; M = March; A = April; M = May; J = June.

Period = two-week interval. The first begins Feb. 2.

only twice during the whole study. In most cases 4 birds (2 pairs) were involved in each encounter. The peak in numbers of aggressive encounters coincided with the two-week period of flock break-up and onset of territorial behaviour in both years.

Table 2 shows the corresponding data from the control area. As on the main study area, before the peak of aggression the birds were observed in flocks, and after the peak they were in pairs. Therefore the break-up of winter flocks and territory formation in the control area coincided with that on the main study area in both years.

TABLE 2.

Number of observed aggressive encounters in
the spring: control study area.

1964		1965	
Date	No.	Date	No.
Jan. 30	0	Feb. 2	0
Feb. 13	0	Feb. 16	0
Feb. 27	4	Mar. 2	5
Mar. 12	2	Mar. 16	2

b) Numerical Results

i) Clutch Size. In the two years of the study the average clutch size was almost the same. In 1964, seventeen clutches were laid (four were second attempts), for a total of 90 eggs, and an average of 5.3 ± 0.42 eggs/clutch. In 1965, seven clutches were counted, giving a total of 38 eggs, or an average of 5.4 ± 0.65 eggs/clutch.

ii) Fertility and Hatching Success. The figures in Table 3 used to calculate the fertility rate (observed totals) are only those obtained from nests where young fledged and were counted. This is because the nests were opened only once, to band the young. To estimate the total mortality occurring on the study area up to the time of hatching, clutches had to be used which were deserted, or destroyed either as eggs or fledglings before I could count them. The average clutch sizes and fertility rates were used to get the unknown figures; these were then included to obtain the Hatching Success (corrected totals).

In 1964, four clutches are added in the Corrected totals: one of 6, one of 3, one of 2, and an uncounted one of 5.3. The hatching success for 1964 was thus $69/89.3$, or 0.773 . In 1965, three clutches were uncounted. Two of these hatched, and the other was destroyed before hatching. Applying average clutch size and fertility rate, the hatching success for 1965 was $(35 + 5.4 + 5.4) - (38 + 5.4 +$

TABLE 3.

Fertility Rate and Hatching Success.

1964				1965		
Week ending	Eggs laid	No. nests	Proportion hatched	Eggs laid	No. nests	Proportion hatched
April 30	0	0	--	7	1	0.86
May 7	20	3	1.00	11	3	0.91
14	25	5	0.96	7	1	1.00
21	7	1	1.00	13	2	0.92
28	3	1	1.00	0	0	--
June 4	8	1	0.88	0	0	--
11	0	0	--	0	0	--
18	5	1	0.60	0	0	--
25	0	0	--	0	0	--
July 2	5	1	1.00	0	0	--
Observed total:	73			38		
Fertility:			0.945			0.921
Corrected total:	89			54		
Hatching success:			0.773			0.833

5.4) = ~~45.1~~/54.2 or 0.845.

iii) Fledging Success. In each year, every brood except one was totally fledged. Since in each case of loss the whole brood as well as a parent disappeared at the same time, this was presumably due to predation. Fledging success was 0.94 in 1964 and 0.89 in 1965.

iv) Juvenile Survival. Until the family groups broke up three to four weeks after fledging, the survival of the young birds could be followed (Table 4). In 1964, of 61 banded juveniles, 50 survived until the break-up. All eleven of the birds which disappeared did so in the first week after fledging: none was seen after a particularly severe storm on 21 May. With this exception, all survived. In 1965, no severe storms occurred immediately after any brood had fledged. One bird disappeared 7 days after it had left the nest; all others were observed until the family groups broke up.

As in other species of Parus (Goodbody, 1952), the young suddenly disperse some three to four weeks after fledging. On the study area this was seen precisely with one family: on 14 June all six young were seen accompanied by the parents; on 15 June the parents were alone in their territory, and two of the young were seen separately, neither of them in the original territory. Since then none of the six young has been seen.

TABLE 4.

Survival of banded young on the study area from the day of fledging.

Week after fledging	1964			1965		
	No. seen during week	Proport- ion surviving	lx	No. seen during week	Proport- ion surviving	lx
0	61	0.8197	1000.0	33	1.0000	1000.0
1	50	1.0000	819.7	33	1.0000	1000.0
2	50	0.9200	819.7	33	0.8788	1000.0
3	46	0.4348	753.1	29	0.5517	878.8
4	20	0.4500	327.4	16	0.2500	484.8
5	9	0.5556	147.3	4	1.0000	121.2
6	5	1.0000	81.8	4	1.0000	121.2
7	5	1.0000	81.8	4	1.0000	121.2
8	5	1.0000	81.8	4	1.0000	121.2
9	5	1.0000	81.8	4	1.0000	121.2
10	5	1.0000	81.8	4	1.0000	121.2

At the time when the banded young left the study area, there was an influx of unbanded birds. These were almost 100% young; they could be distinguished from adults by their unworn plumage and by their calls (Odum, 1942). This exchange of birds was very extensive: of 61 banded young in 1964, only five remained in the study area by September. In 1965, of 35 marked young only four remain in area to date (Fig. 3). However, without a much more extensive marking programme, no accurate measure of juvenile survival after family break-up can be made.

v) Adult Survival. The rate of survival of chickadees from September to the next autumn in the study area was not constant (Table 5; Figs. 4-6). When the survival rate is calculated for two-week periods throughout the year, there is one period when the rate is significantly lower than those in any adjacent periods. The statistical test used here was to obtain 95% binomial confidence intervals on the fortnightly survival rates. These were taken from Table A.15A (p. 458) of Steel and Torrie (1960). As the confidence interval for the critical fortnight's rate does not overlap those of adjacent rates in either year, it can thus be said to be significantly different from adjacent rates (Figs. 4 and 5). In 1964 this two-week period was the end of February; in 1965 it was the first two weeks in March. In both years the period of loss was correlated exactly with the onset of territorial behaviour (Tables 1 and

TABLE 5.

Survival of marked birds on the study area from
1 September.

1963-64				1964-65		
Two week period	No. seen during period	Proport- ion surviving	lx	No. seen during period	Proport- ion surviving	lx
SS				11	0.909	1000
SS				10	1.000	909
SO				4	1.000	909
OO				12	1.000	909
ON				9	1.000	909
NN				11	0.917	909
ND	4	1.000	1000	13	1.000	834
DD	8	1.000	1000	30	0.909	834
DJ	13	1.000	1000	20	0.909	758
JJ	21	0.875	1000	26	0.929	689
JF	29	0.935	875	37	1.000	640
FF	34	1.000	818	44	0.978	640
FM	23	0.676	818	48	0.941	626
MM	26	1.000	553	28	0.583	589
MM	25	1.000	553	26	0.929	343
MA	24	1.000	553	24	1.000	319
AA	22	0.956	553	20	0.952	319
AM	24	0.960	529	19	0.950	304
MM	21	0.950	508	16	0.941	289
MJ	19	0.905	482	15	0.937	272
JJ	10	0.833	436	15	1.000	255
Jj	7	0.875	363	11	0.917	255
jj	9	1.000	318	7	1.000	234
jA	11	1.000	318	9	1.000	234
AA	12	0.857	318			
AA	6	0.857	273			
AS	8	0.889	234			
SS	9	1.000	208			
SO	4	1.000	208			
OO	9	1.000	208			
ON	5	1.000	208			
NN	9	0.900	208			
ND	8	1.000	187			

Note: S=September; O=October; N=November; etc.

2): before this period the birds were all in winter flocks, and afterward they were in territorial pairs.

Throughout this period and the following week over 20 unbanded birds were seen in the study area in 1964, and over 15 in 1965. As far as I could tell, none of these unmarked birds remained to breed; that is, each banded bird that remained to breed with an unbanded bird was associating with an unbanded bird in the winter flock before spring break-up. This then indicates that the same process was occurring in surrounding areas.

I cannot assume that all the birds which disappeared from the study area died - especially not those which disappeared during the critical fortnight in the spring. All I know is that they remained neither in the area, nor did they own territories immediately surrounding it. Thus, they no longer survived on my study area.

The proportion of adults found after the breeding season was also low, especially in 1964. This drop was not as sudden as that in either spring. It is known that adult chickadees go through a period of moult after breeding, and it is suggested that this is a time of considerable physiological strain for the individuals. However beyond this correlation there is no direct evidence supporting the idea that the moult was responsible for this period of loss. I suspect that all birds disappearing during this time did indeed die, although I cannot prove this. Evidence supporting it, however, is that no unbanded birds

were recorded as entering the study area at this time. This was based on differences in plumage and in voice.

vi) Excess Birds During Breeding. In each year of the study there was one unmated female in the study area during the breeding season. These birds were allowed to range over several territories, and in all observed cases when the owners were encountered, the unmated bird gave the begging call (Odum, 1942).

No excess males were recorded during either breeding season. Evidence that there was none is that in both years at least one male died early in the breeding season (just before or during incubation) and in each case the territory was not claimed by a new male, and the female remained unmated for the rest of the year.

DISCUSSION

Three assumptions have been made in this study. The study area was assumed to be favourable habitat, i.e. production of young was expected to exceed adult losses, thus resulting in surplus birds. This condition was necessary for this study. Also, it was assumed that the study population was a representative sample of populations of this species in favourable habitats. Finally, populations of Black-capped Chickadees were assumed to behave similarly to those of other passerine species of similar ecology, such as titmice.

Adult losses during the following summer, autumn and winter were considerably less than the number of young fledged in the study area. Although almost all of these young disappeared from the area during juvenile dispersal, subsequent banding data indicate that their place was taken by an apparently similar number of unbanded young. (It is peculiar that in 1964 the number of immigrants was so close to the number of emigrants. Nothing is known of any mechanism that might have been responsible for this result, indeed, in 1965 immigration may have exceeded production.) However, the study area can still be called "favourable" habitat, for not only was a surplus of young produced in the area, there was also a surplus present at the beginning of autumn.

The drop in numbers which effected the removal of the surplus birds and thus regulated the breeding

density of the study population occurred in the spring, and was correlated with the break-up of winter flocks and the onset of territorial behaviour. This change in behaviour is a general factor and is characteristic of all Black-capped Chickadee populations which have been studied (Brewer, 1961; Tanner, 1952; Odum, 1941a; McCamey, 1962). It is also characteristic of some other Paridae (Tanner, 1952; Brewer, 1961; and Dixon, 1963: Carolina Chickadee; Root, 1964: Chestnut-backed Chickadee; Kluyver, & Tinbergen, 1953; Gibb, 1960: Great Tit; Gibb, 1960: Blue and Coal Tits).

It has long been suspected that territorial behaviour in spring regulates the size of certain species' breeding populations. Tompa (1962) found that territorial behaviour did regulate the breeding numbers of Song Sparrows on a small island (Mandarte Island, B.C.). Jenkins, Watson & Miller (1963) showed that in their study areas in northeast Scotland territorial behaviour regulated the size of the breeding population of Red Grouse. Watson (1965) working on Ptarmigan in the Cairngorms, Scotland, wrote,

"During 5 years when winter counts were done, numbers stayed fairly constant from autumn till spring, but decreased suddenly in March or April, following the break-up of flocks and the onset of vigorous territory defence."

Concerning territories in general, Hinde (1956) wrote,

"... the observations that territory owners are

forced to defend their territories from encroachment, that some attempts to settle are unsuccessful, and that some individuals are forced to breed in sub-optimal habitats, strongly suggest that territory regulates the density of many species in the most favoured areas. Proof is lacking." (p. 354)

Yet as far as titmice are concerned, it seems that no attempt has been made to prove or disprove Hinde's supposition. Although it has been demonstrated in some species, Gibb, and Perrins seem to have ignored it.

If territorial behaviour is indeed the variable which limits the breeding density of chickadees, it ought to apply to some titmice as well. Let us now consider the studies on titmice population ecology, to see if territorial behaviour seems to be a relevant variable in those populations too.

Gibb (1960) claims to have shown that the tit populations in Thetford Chase were controlled by winter food shortage. There are several objections to this conclusion. His populations were not marked, and apparently no allowance was made for the fact that nearby populations were not totally stable (Gibb, 1950). Also, his counts were only monthly: "... the monthly census in winter should be sufficiently accurate to indicate the general level of the population and to reveal major seasonal changes in the number of each species." (Gibb, 1960; p. 168) His graphs on pp. 170 and 191 (both Coal and Blue Tits) show a drop in the last month before breeding in almost every year; this drop, he claims, is the result of lack of food at that time, although he has no direct evidence for this.

Finally, he bases his conclusions to a great extent on a graph (1960; p. 195) which shows the correlation between minimum winter invertebrate food stock and "percent survival" of the Coal Tit. Actually he did not have any survival data; all he had was the proportion of fall numbers present in the spring, based on two counts: one at the end of September and the other in April. Yet he says of this correlation that it "... is so striking that it seems almost unnecessary to look for alternatives." (1960; p. 195). In fact he is so convinced by this correlation that he has accepted it without looking seriously for alternative explanations.

The second major hypothesis was first proposed by Perrins (1963), when he showed that in Marley Wood the higher the proportion of juvenile Great Tits in the winter population, the higher the breeding population the following year. However, the actual winter counts from Marley Wood were not given, and numbers apparently were not measured, the proportion of juveniles having been obtained by sampling. Thus, a low proportion may mean simply a high adult survival. It is possible that adults are more aggressive than yearlings at the onset of territorial behaviour, so that the more adults there are, the fewer territories there are. This is borne out by my data: the three largest territories in the study woods in 1965 were held by the only three intact pairs surviving from the 1964 season. Thus, until actual winter counts are made, it is unknown whether the juvenile

or the adult survival is of more importance in Marley Wood, and finally, since no winter censuses were made at all in Marley Wood, there are no data on the temporal pattern of winter mortality in this study.

The third hypothesis suggests that spring territorial behaviour limits breeding densities. This is by no means a new idea, and has been demonstrated in species of some other families. It was first put forth in reference to titmice in 1953 by Kluyver & Tinbergen, while they were proposing a buffer mechanism of poor habitats for excess birds, and has up till now not been properly investigated in the genus Parus. Lack (1964) writes that in Marley Wood, territorial behaviour plays no effective part in the regulation of the breeding density of the Great Tit, although he writes, "Until 2 years ago, one might possibly have argued that territorial behaviour set a limit to the number of great tits breeding in Marley ..." (p. 172). The reason he rejects territorial control is that 86 pairs, almost twice as many as usual, bred in Marley Wood in 1961. The assumption Lack makes here is that territories are a fixed size regardless of other variables. However, what controls the size of territories is unknown. The fact that different numbers of territories are established in different years is irrelevant; the relevant point is whether or not there are losses associated with territorial behaviour. Lack gives the estimated maximum population for the previous winter: 304 individuals. As

only 86 pairs bred the next spring, the estimated loss is 132, which is more than the maximum number believed to have been present in five of the ten winters quoted. These excess birds must have disappeared between October and April; but again there are no data on the time these losses occurred. Lack therefore has no evidence against the view that many birds disappeared with the onset of territorial behaviour in spring.

The last theory has one great merit: it is more general than the other two put forth. The change from flocking to territorial behaviour has been reported in every population of chickadees studied, whereas severe winter food shortage, or severe summer conditions resulting in low juvenile survival, happen only some years in some areas. It is true that if all excess birds are removed by these or other factors before spring, this change in behaviour will still occur although it will have no numerical effect.

An hypothesis is of very little use if it cannot be tested. The hypothesis that territorial behaviour regulates breeding densities in favourable habitats has withstood the first test of being confirmed over two successive years. However, it is necessary that further tests be possible. One possible method is a series of experiments using several plots from which birds are removed at different times of year. The predictions of this hypothesis are that if the birds are removed after

the start of laying, the only invasion will result from neighbouring pairs' expanding their territories. However, if the birds are removed from a plot during the time of change from flocking to territorial behaviour, or within a period of roughly two to three weeks thereafter, there should be an invasion by excess birds driven off from surrounding areas (providing there has been good survival in these areas) and some of these invading birds should claim territories and remain to breed, as Stewart & Aldrich (1951) and Hensley & Cope (1951) found with wood warblers.

CONCLUSIONS

The factor preventing continual increase in the study population in a favourable habitat was the change in behaviour from flocking to territorial, with the resulting increase in aggressivity of individuals. Because this change in behaviour is a general factor which has been observed in all studied populations of Black-capped Chickadees and also in those of many other species, it is suggested that this factor may be the one controlling the breeding densities of other species of similar ecology as well, providing they are in favourable environments.

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FIGURE 1. Flock ranges (A) and breeding territories (B) on the study area: 1963-64.

Numbers: banded birds alive in each flock Feb. 12, 1964.

FIGURE 2. Flock ranges (A) and breeding territories (B) on the study area: 1964-65.

Numbers: banded birds alive in each flock Feb. 14, 1965.

FIGURE 3. Survival of banded young on the study area from the day of fledging.

FIGURE 4. Minimum survival rates and 95% confidence intervals for each two week period in 1963-64.

FIGURE 5. Minimum survival rates and 95% confidence intervals for each two week period in 1964-65.

FIGURE 6. Survival of marked birds on the study area from Sept. 1st.