

SEASONAL CHANGES IN THE SURVIVAL OF THE BLACK-CAPPED CHICKADEE

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This study attempts to answer the following general question: What prevents continual increase in a population whose environment is apparently favorable? In such an environment, production (and immigration) must exceed losses (including emigration). If under these circumstances the population does not increase, then "surplus" birds must be present at some time during the annual cycle. In species in which all birds present in the spring do breed, any mechanism of population control must act to remove these surplus birds.

The Black-capped Chickadee (*Parus atricapillus*) seemed well suited for a study of this kind. It nests in holes (and boxes) and comes readily to feeding stations, where it can be trapped. It has a fairly large clutch size (Peterson, 1961, gives a range of 4 to 9 eggs). It reaches maturity and breeds in the first year after hatching. Like many other members of the genus *Parus*, it is strongly territorial during the breeding season, but spends the rest of the year in flocks, thus exhibiting two distinct seasonal modes of behavior toward other members of the same species. In Vancouver, British Columbia, where this study was conducted, it is a nonmigratory resident.

It is likely that in any environment the survival rate will not be constant; *i.e.*, there will be certain periods in the year when sudden decreases in numbers occur. The object of this study was to find out when these decreases occurred, and to attempt to discover their causes.

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 arbitrarily to include the ranges of as many flocks as could be censused each week, and were not physically isolating. However, as interflock exchange of individuals in this study was extremely rare, the boundaries seemed to be in effect behaviorally isolating.

The area was part of a residential district and included strips of woods along the east and west sides. There were many mature deciduous trees in the gardens throughout the residential part of the study area, some of which were used by chickadees as nest sites. The woods of the area were second-growth deciduous woods, consisting almost entirely of red alder (*Alnus rubra*). This tree was the only kind used for nest sites by chickadees in the study woods. To make the area as favorable as possible, nest boxes were put up throughout the area and feeding stations were maintained during the winters.

Since it could be argued that this population was not living under sufficiently natural conditions, observations were also made in a natural forest one and one-quarter miles from the main study area. This was called the control area. Its woods were second-growth mixed forest, the canopy being approximately 55 per cent deciduous and 45 per cent coniferous. As this area contained many old alders and maples, there was again an excess of nest sites. The control area was roughly the same size as the main study area, and each winter supported at least three flocks. Since each flock contained 6 to 12 chickadees, flock break-up in the spring was easily observed even though the birds were unbanded.

METHODS

During both winters of the study (1963-64, and 1964-65) chickadees were captured with mist nets placed near feeding stations. This method of capture was successful only from early November to the end of February, the only period when chickadees came regularly to the feeders. Each marked bird was given a numbered aluminum band supplied by the Canadian Wildlife Service, and from one to three colored, plastic bands. Six readily distinguished colors were used: red, yellow, light green, dark blue, orange, and black. Each individual was given a different color combination. The young were banded in the nest when they were approximately 10 days old.

Sight records of the marked population were made at least once weekly during the project. The presence and behavior of each marked individual were recorded, as were the locality and composition of the flock. One whole morning's observations were made every two weeks throughout both winters on the control area. Estimates of the numbers and observations on the behavior 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.

Forty-two nest boxes were put up in the main study area. Of these, 33 were placed in the residential part of the study area during 1964, and the remaining nine were added in the first week of March 1965, 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 boxes more acceptable to chickadees (Drury, 1958; Kluijver, 1961), since this species normally excavates its own nest hole in soft wood. The boxes were placed at varying heights (most between 7 and 15 feet) and faced in varying directions. All were attached to the main trunk of a tree at least four inches in diameter. These were found to be acceptable to the chickadees; five were used in 1964 and two in 1965, while several others had their sawdust excavated but were not occupied by nesting chickadees.

Feeding stations were maintained throughout both winters on the main study area. The control area was provided with neither food nor nest boxes.

RESULTS

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.

Territory formation. There was a period in the spring not exceeding two weeks in each year when the change from flocking to territorial behavior 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, except at feeding stations. During the period of break-up, however, 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 on defended territories (except for one unmated female each year which was tolerated by territorial pairs). The lower part of figure 3 shows the spring pattern of observed aggressive encounters in the study areas in each year. An "aggressive encounter" was nearly always a prolonged chase accompanied by "fighting notes" and "dominance notes" (Odum, 1942). Actual contact between aggressive chickadees was observed only twice during the entire study. In some pairs only one bird, not necessarily the male, was the main aggressor. However, in

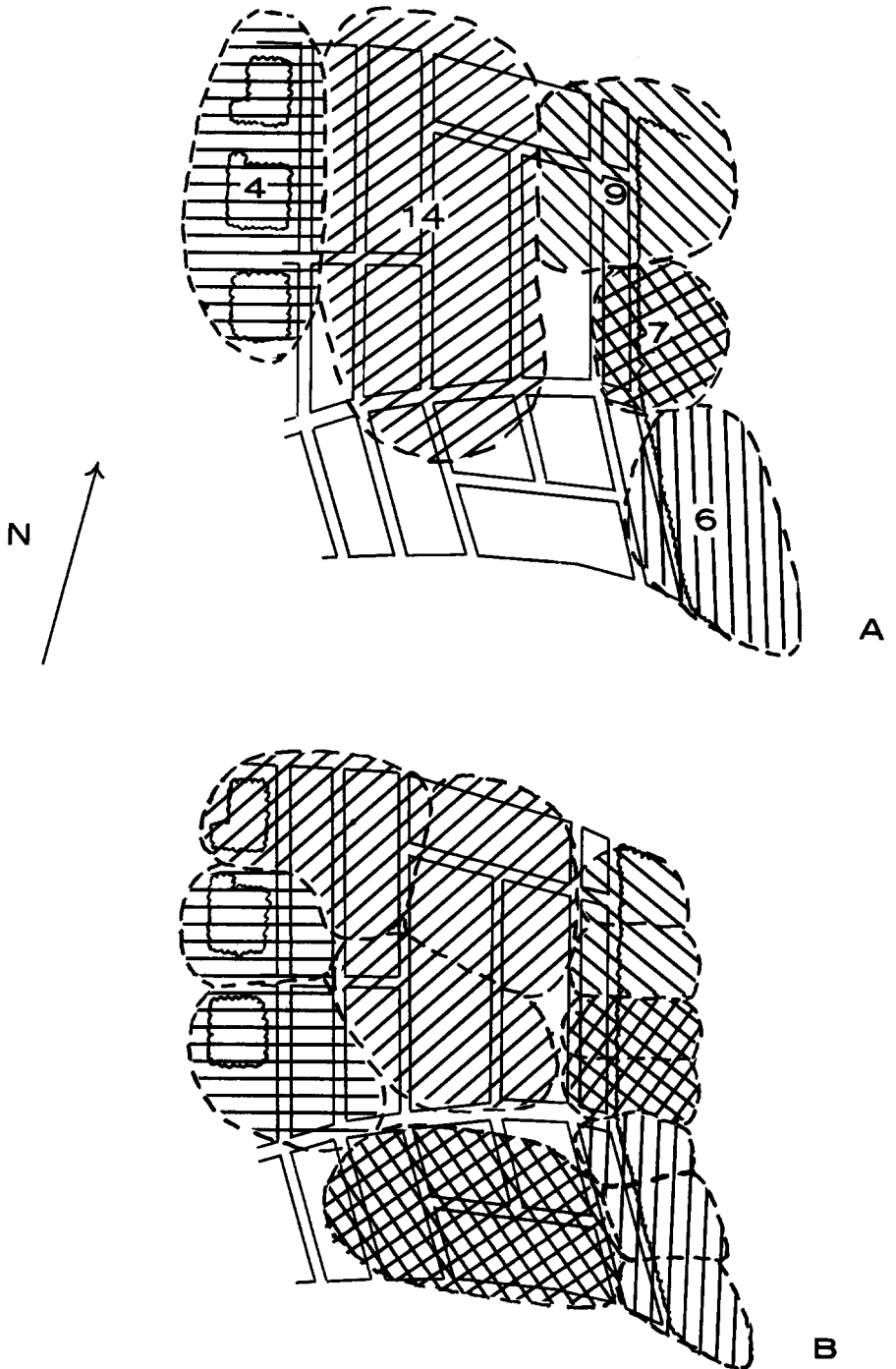


Figure 1. Flock ranges (A) and breeding territories (B) on the study area in 1963-64. Numerals: banded birds alive in each flock, 12 February 1964.

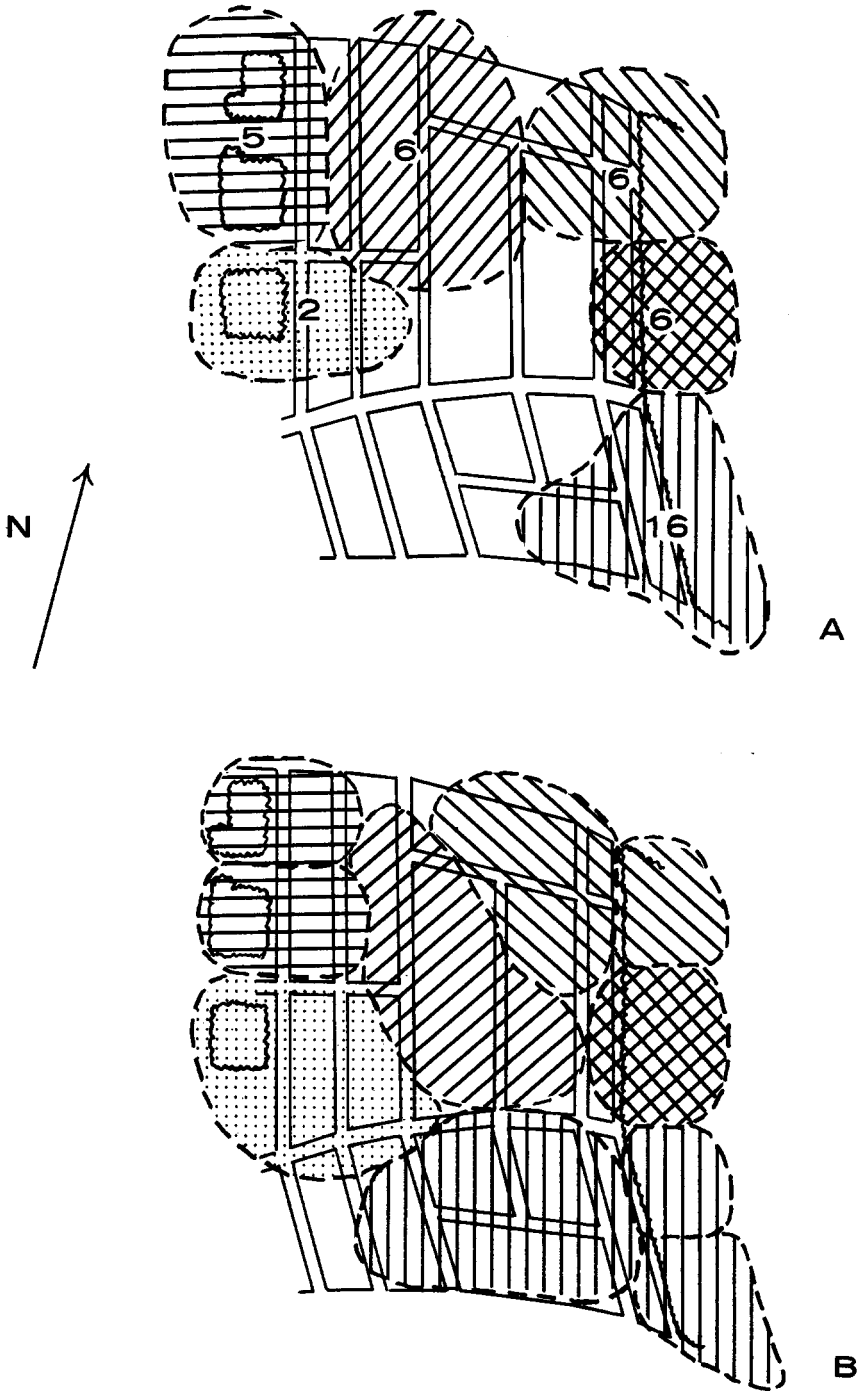


Figure 2. Flock ranges (A) and breeding territories (B) on the study area in 1964-65. Numerals: banded birds alive in each flock, 14 February 1965.

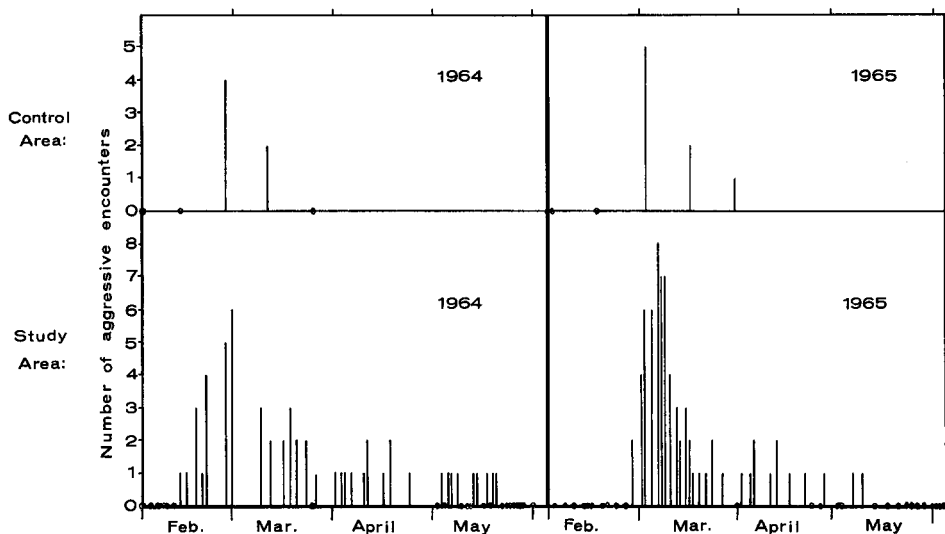


Figure 3. Number of aggressive encounters observed in the spring.

most cases four birds (two pairs) were involved in each encounter. Thus six fights means that about 24 birds were involved. The peak in numbers of aggressive encounters coincided with the two-week period of flock break-up and the onset of territorial behavior in both years.

The upper part of figure 3 shows the corresponding data from the control area. As on the main study area, before the peak of aggression the birds were in flocks, and after the peak they were in pairs. The break-up of winter flocks and territory formation in the control area apparently coincided with that on the main study area in both years.

Clutch size. The nests were opened only once, to band the young. It was assumed that all eggs that did not hatch remained unbroken in the nest, and thus could be counted. Up to three unhatched eggs have been found intact in nests with several large fledglings; also no evidence of broken eggs was found in any nest that contained living young. There was no significant correlation between clutch size and time of year in either 1964 or 1965. In the two years of the study the average clutch size was almost the same. In 1964, 17 clutches were laid (four were second attempts) for a total of 89 eggs (mean \pm SE = 5.3 ± 0.42 eggs/clutch). In 1965, seven clutches were counted, giving a total of 38 eggs (mean \pm SE = 5.4 ± 0.65 eggs/clutch). There were no cases of second broods on the study area in either year, although they did occur in both years in nearby residential areas less than four miles away from the study area.

Fertility and hatching success. The data in table 1 used to calculate the fertility rate (observed totals) are those obtained only from nests where young fledged and were counted. This is because the nests were opened only once, to band the young. Thus if predation occurred before the young were ready to be banded, no data were obtained from the nest. To estimate the total mortality occurring on the study area up to the time of hatching, clutches had to be included which were deserted or destroyed either as eggs or fledglings before I could count them. The average clutch

TABLE 1
FERTILITY RATE AND HATCHING SUCCESS

Week ending	1964			1965		
	Eggs laid	No. nests	Proportion hatched	Eggs laid	No. nests	Proportion hatched
30 April	0	0	—	7	1	0.86
7 May	20	3	1.00	11	3	0.91
14 May	25	5	0.96	7	1	1.00
21 May	7	1	1.00	13	2	0.92
28 May	3	1	1.00	0	0	—
4 June	8	1	0.88	0	0	—
11 June	0	0	—	0	0	—
18 June	5	1	0.60	0	0	—
25 June	0	0	—	0	0	—
2 July	5	1	1.00	0	0	—
Observed total	73			38		
Fertility			0.945			0.921
Corrected total	89			54		
Hatching success			0.773			0.845

sizes and fertility rates were used to calculate estimates of these unknown figures; these were then included to obtain the "hatching success" (corrected totals) in table 1.

In 1964 four clutches are added in the corrected totals: one of 6, one of 3, one of 2 eggs, and an uncounted estimate 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 $(35 + 5.4 + 5.4) \div (38 + 5.4 + 5.4 + 5.4) = 45.8/54.2$ or 0.845 .

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.

Nesting success. Nesting success (number of young fledged per pair) was almost identical in the two years of the study. In 1964, 13 pairs fledged 65 young, an average of 5.00 young/pair. In 1965 the seven nests counted fledged 34 young, an average of 4.99 young/pair.

Juvenile survival. Until the family groups broke up three to four weeks after fledging, the survival of the young birds could be followed (see fig. 4). In 1964, of 61 banded juveniles, 50 survived until the break-up. All 11 of the birds that disappeared did so in the first week after fledging; none of them was seen after a particularly severe storm on 21 May. At the time of this storm, only 15 young had left their nests; thus only four survived the storm. These four were the same age as four that disappeared. Apart from these 11 deaths, all birds survived. In 1965 no severe storms occurred immediately after any brood had fledged. One bird disappeared seven days after it had left the nest; all others were observed until the family groups broke up.

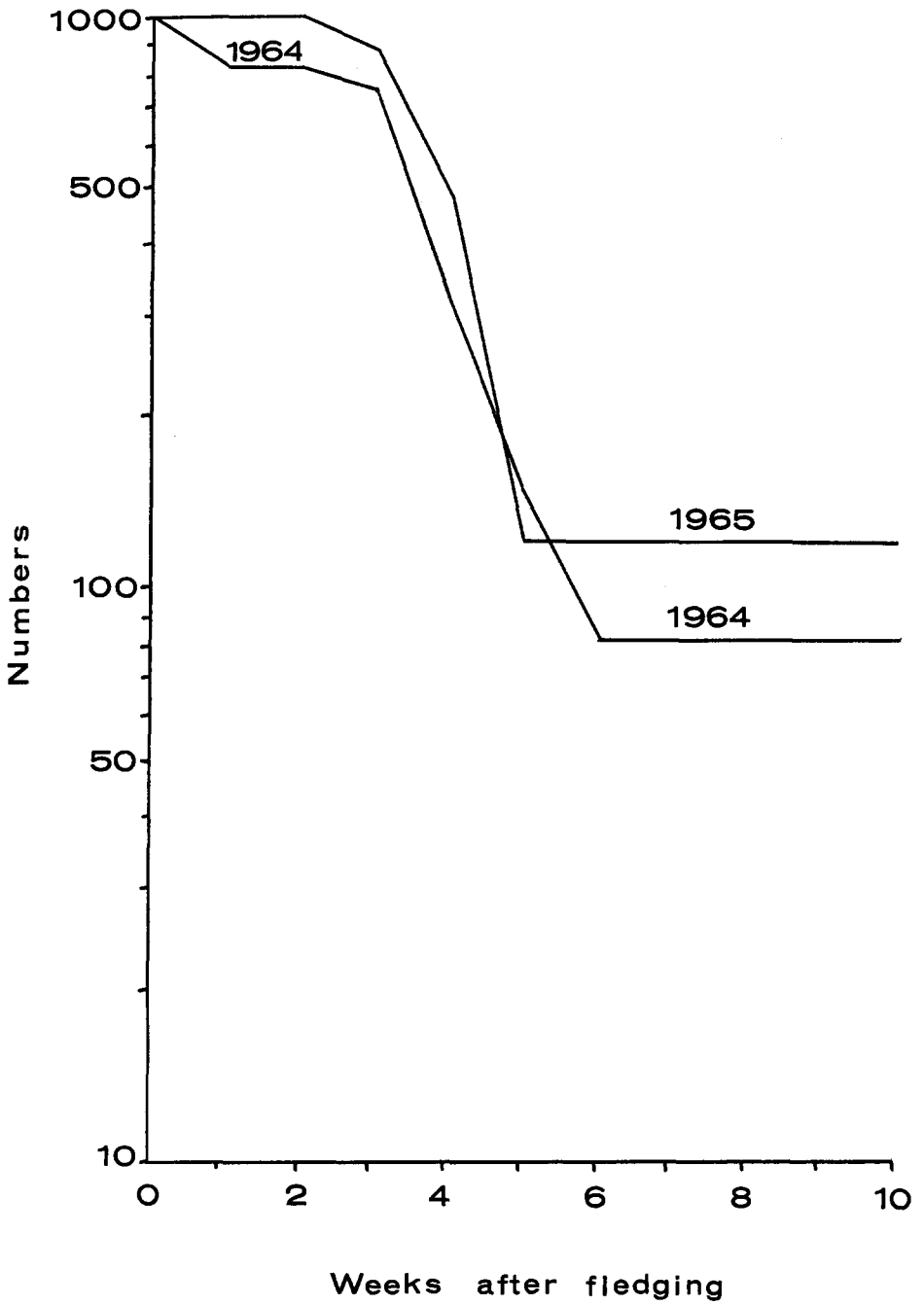


Figure 4. Survival of banded young on the study area from the day of fledging.

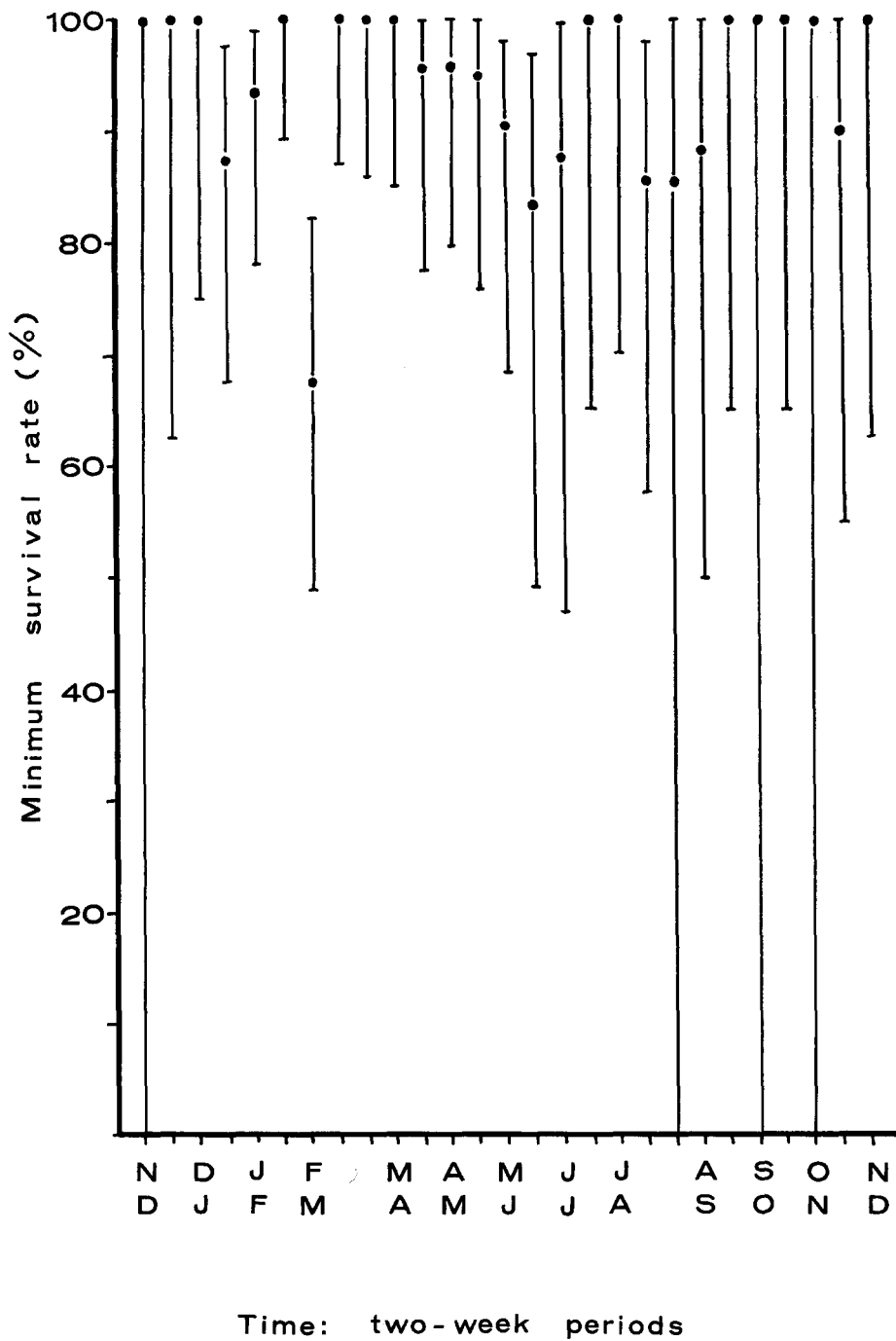


Figure 5. Minimum survival rates and 95 per cent confidence intervals for each two-week period in 1963-64. Periods begin 24 November 1963.

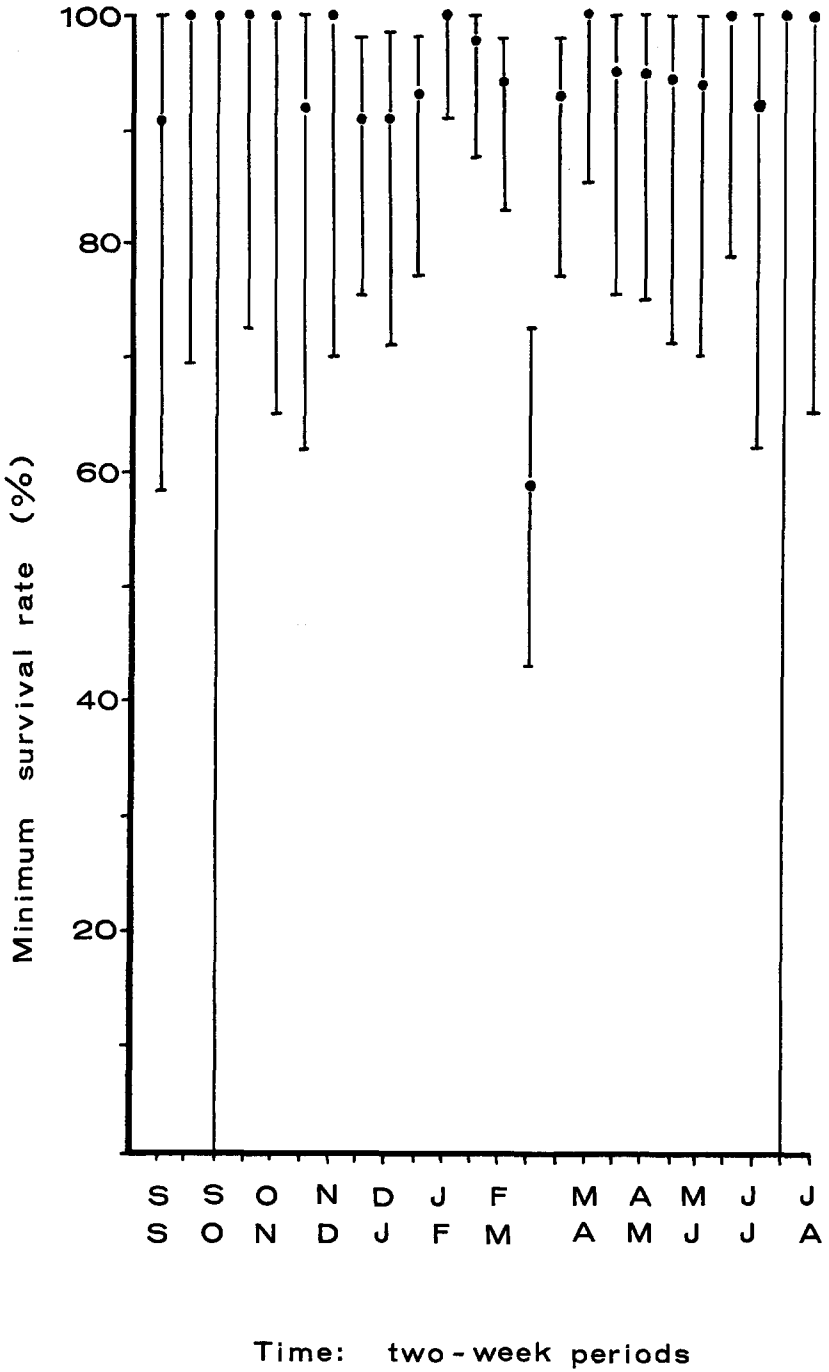


Figure 6. Minimum survival rates and 95 per cent confidence intervals for each two-week period in 1964-65. Periods begin 1 September 1964.

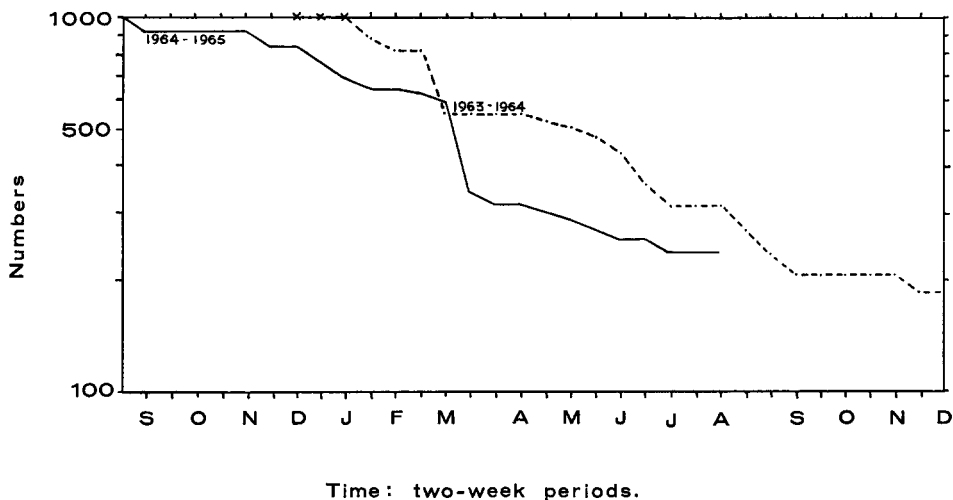


Figure 7. Survival of marked birds on the study area from 1 September.

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 closely observed 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.

At the time when the banded young left the study area, there was an influx of unbanded birds. These were almost 100 per cent young, 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 remained in the area by September (fig. 4). However, without a much more extensive marking program, no accurate measure of juvenile survival after family break-up can be made.

Of the five banded young remaining on the study area in September 1964, none nested in the area in 1965. However, one of the four remaining in September 1965 (a male) remained and bred in a nest box in 1966.

Survivorship. Survivorship data are presented in the form of lx curves (figs. 4 and 7). Nice (1937) and Lack (1943) were among the first to apply these curves to songbirds, and Deevey (1947) presents an excellent review of their ecological uses. The numbers plotted in an lx curve indicate the proportion of birds surviving to the beginning of a particular time (or age) interval; in figures 4 and 7 a straight line would indicate that a constant fraction of the surviving birds die (or disappear) in the next unit of time. Since family groups of chickadees are relatively easy to find and observe, counts were complete for banded young between the time they left the nest and family flock break-up. Hence no special problems arose for juvenile survival. However, in the case of adults, some individuals were missed in almost every two-week period. 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. For example, of 11 birds observed in the first two weeks of

September 1964, two were known to be alive almost a year later—an observed minimum survival rate of 0.18. The rate calculated from the individual two-week samples is slightly greater than this (0.23). Other intervals have been similarly examined, and any bias that may be present appears to be concealed by errors of sampling.

Adult survival. The rate of survival of chickadees from 1 September onward is taken here to be a measure of adult survival. By September juveniles could no longer be distinguished consistently from adults in the field. It is assumed that any differences in survival between juveniles and adults occurs only before the establishment of winter flocks. Thus any chickadee surviving on the study area by September has been considered an "adult."

During the winter of 1963-64, 44 chickadees were banded. Of the nestlings banded on the study area in 1964, five remained on the study area by September 1964. When these five are added to the 17 surviving adults and 38 birds banded during the next winter, we reach a total of 60 banded birds present on the study area in the winter of 1964-65.

The rate of adult survival in the study area was not constant in either year (figs. 5-7). 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 is to obtain 95 per cent binomial confidence intervals on the fortnightly survival rates (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. 5 and 6). 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 coincided exactly with the onset of territorial behavior (fig. 3); 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 chickadees were seen in the study area in 1964, and over 15 in 1965. In neither year was there such a high number of unbanded birds present in the winter flocks during the weeks just before this critical period. As far as I could tell, none of these unmarked birds remained to breed. There were no unbanded pairs in either year on the study area, and 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. Probably these unbanded wanderers are equivalent to the birds that had spent the winter in the study area and then disappeared in the spring. This would then indicate that the same process was occurring in areas surrounding the study area.

I cannot assume that all the birds that disappeared from the study area died—especially not those that disappeared during the critical fortnight in the spring. However, they were not observed again in the area, and did not own territories immediately surrounding it. Hence they no longer survived on the study area.

In 1964 many of the adults that had bred on the study area did not survive to the first of September. This drop in survival was not as sudden as that in either spring. Since the time of this drop coincided with the period of adult molt, it was at first suggested that this drop was caused by the physiological strain of molting. Certainly these birds disappeared only after breeding was over; they were never seen anywhere again, and no unbanded adults were recorded as entering the study area during this time. However, no correspondingly severe drop in adult numbers occurred during the period of adult molt in 1965. Thus the cause of the 1964 drop remains unknown.

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). The unmated female of 1964 paired and nested on the study area in 1965.

No excess males were recorded during either breeding season. 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 summer. This seems to indicate that the situation found by Stewart and Aldrich (1951) for warblers did not exist for chickadees in this study area.

DISCUSSION

Although no immigration was observed during either winter, there were more birds present each year in winter flocks on the study area just prior to the onset of territorial behavior than there were during breeding. Adult losses during the following summer, autumn, and winter were considerably less than the number of young fledged in the study area each year. Although almost all of these young disappeared from the area during juvenile dispersal, their place was taken (again through juvenile dispersal) by an apparently similar number of unbanded young in 1964, and in 1965 such immigration may have exceeded production. Thus the study area can be called "favorable." Not only was a surplus of young produced in the area, but there was also a surplus present at the beginning of autumn when winter flocks were formed.

The drop in numbers that effected the removal of these 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 behavior. This change in behavior is characteristic of all Black-capped Chickadee populations that have been studied (Odum, 1941a; Tanner, 1952; Brewer, 1961; McCamey, 1962; and others). It is also characteristic of some other Paridae (*Parus carolinensis*: Tanner, 1952; Brewer, 1961; and Dixon, 1963; *P. rufescens*: Root, 1964; *P. major*: Kluyver and Tinbergen, 1953; Gibb, 1960; *P. caeruleus* and *P. ater*: Gibb, 1960).

It has long been suspected that territorial behavior in the spring regulates the size of certain species' breeding populations (Howard, 1920). Tompa (1962) found that territorial behavior did regulate the breeding numbers of Song Sparrows on a small island (Mandarte Island, B.C.). Jenkins, Watson, and Miller (1963) showed that in their study area in northeast Scotland territorial behavior 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 suboptimal habitats, strongly suggest that territory regulates the density of many species in the most favoured areas. Proof is lacking.

There are apparently three main schools of thought as to what factors have the most control over titmouse breeding density. 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. 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." His graphs (pp. 170 and 191) for *Parus caeruleus* and *P. ater* 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 conclusion to a great extent on a graph (p. 195) that shows the correlation between minimum winter invertebrate food stock and "percent survival" of the Coal Tit (*P. ater*). This survival rate was obtained from the proportion of fall numbers present in the spring, based on only two counts: one at the end of September and the other in April. This method does not take into account any effects of immigration or emigration that might occur; also it gives no information on the temporal pattern of these losses. Yet Gibb says of this graph that the correlation ". . . is so striking that it seems almost unnecessary to look for alternatives."

The second major hypothesis was first proposed by Perrins (1963), when he demonstrated 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 behavior—the more adults there are, the fewer territories. 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 it is possible that adult survival, rather than juvenile losses, is of major importance in Marley Wood. Again, since no winter censuses were apparently made in Marley Wood, there are no data on the temporal pattern of winter mortality in Perrins' study.

The third hypothesis suggests that spring territorial behavior limits breeding densities. This is by no means a new idea, and has been demonstrated in species of several families. It was first put forth in reference to titmice in 1953 by Kluyver and Tinbergen, while they were proposing a buffer mechanism of poor habitats for excess Great Tits, and has up till now not been investigated in the genus *Parus*, although Wynne-Edwards (1962:152) mentions the significance of territoriality and breaking up of tit flocks in population control. Lack (1964) claims that in Marley Wood territorial behavior plays no effective part in the regulation of the breeding density of the Great Tit, although he writes (p. 172), "Until 2 years ago, one might possibly have argued that territorial behaviour set a limit to the numbers of great tits breeding in Marley. . . ." The reason that 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 of 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 inconclusive; the relevant point is whether or not there are losses associated with territorial behavior. Lack gives the estimated maximum population for the previous winter as 304 individuals. Since 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 10 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 behavior in the spring.

The last theory has one great merit: it is more general than the other two. The change from flocking to territorial behavior 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. Where all excess birds are removed by these or other factors before the spring, this change in behavior will still occur although it will have no numerical effect.

A hypothesis is of very little use if it cannot be tested. The hypothesis that territorial behavior regulates breeding densities in favorable habitats has withstood the first test of being confirmed in this study over two successive years. However, it is desirable that further tests be made. 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 neighboring pairs' expanding their territories. However, if the birds are removed from a plot during the time of change from flocking to territorial behavior, or within a period of roughly two to three weeks thereafter, there should be an invasion by excess birds driven off surrounding areas (providing there has been good survival in these areas), and some of these invading birds should claim territories and remain to breed.

Providing that territorial behavior is indeed the limiting factor in chickadee populations, this only leads to a further problem, for as yet we still do not know what determines the size of the territories.

SUMMARY

A population of Black-capped Chickadees living in a favorable environment was color-banded, and its survival on the study area was followed over a two-year period. A weekly census of the population was made throughout 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 one-quarter miles from the main population.

Nesting success was high in both years, with 5.00 young/pair being fledged in 1964 and 4.99 young/pair in 1965. Juvenile survival until family break-up was almost 100 per cent in each year; juvenile survival until September seemed to be high. Adult losses did not occur steadily throughout the year; rather there was a sharply defined period of high mortality, emigration, or both, at the time of the change from flocking to territorial behavior in the spring. With the exception of one unmated female in each year, every bird that remained after this critical period bred or attempted to breed; hence this change in behavior in the spring evidently removed surplus birds from the area, and thus prevented continual increase in the population. Breeding populations of other species with similar ecology, *e.g.* other members of the same genus, may also be limited by similar behavior patterns.

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LITERATURE CITED

- BREWER, R. 1961. Comparative notes on the life history of the Carolina Chickadee. *Wilson Bull.*, 73:348-373.
- BREWER, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina chickadees. *Auk*, 80:9-47.
- CHITTY, D. 1952. Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936-9. *Phil. Trans. Royal Soc., B.*, 236:505-552.
- DEEVEY, E. S., JR. 1947. Life tables for natural populations of animals. *Quart. Rev. Biol.*, 22: 283-314.
- DIXON, K. L. 1963. Some aspects of social organization in the Carolina Chickadee. *Proc. XIII Intern. Ornithol. Congr.*, 240-258.
- DRURY, W. H., JR. 1958. Chickadees and nest boxes. *Massachusetts Audubon Society Bull.*, November: 1.
- GIBB, J. A. 1960. Populations of tits and Goldcrests and their food supply in pine plantations. *Ibis*, 102:163-208.
- GOODBODY, I. M. 1952. The post-fledging dispersal of juvenile titmice. *Brit. Birds*, 45:279-285.
- HINDE, R. A. 1956. The biological significance of the territories of birds. *Ibis*, 98:340-369.
- HOWARD, H. E. 1920. *Territory in bird life*. John Murray, London.
- JENKINS, D., A. WATSON, and G. R. MILLER. 1963. Population studies on Red Grouse, *Lagopus lagopus scoticus* (Lath.), in north-east Scotland. *J. Anim. Ecol.*, 32:317-376.
- KLUIJVER, H. N. 1951. The population ecology of the Great Tit, *Parus m. major* L. *Ardea*, 39:1-135.
- KLUYVER, H. N. 1961. Food consumption in relation to habitat in breeding chickadees. *Auk*, 78:532-550.
- KLUYVER, H. N., and L. TINBERGEN. 1953. Territory and the regulation of density in titmice. *Arch. Neerl. Zoöl.*, 10:265-289.
- LACK, D. 1943. *The life of the Robin*. H. F. & G. Witherby, London.
- LACK, D. 1964. A long-term study of the Great Tit (*Parus major*). *J. Anim. Ecol.*, 33, Jubilee Symposium Suppl.:159-173.
- MCCAMEY, F. JR. 1962. Survival and age structure in a sample population of the Black-capped Chickadee. Ph.D. dissertation, University of Connecticut.
- NICE, M. M. 1937. Studies on the life history of the Song Sparrow. Vol. I. A population study of the Song Sparrow. *Trans. Linn. Soc. N.Y.*, 4:1-247.
- ODUM, E. P. 1941. Annual cycle of the Black-capped Chickadee. 1. *Auk*, 58:314-333.
- ODUM, E. P. 1942. Annual cycle of the Black-capped Chickadee. 3. *Auk*, 59:499-531.
- PERRINS, C. 1963. Survival in the Great Tit, *Parus major*. *Proc. XIII Intern. Ornithol. Congr.*, 717-728.
- PETERSON, R. T. 1961. *A field guide to western birds*. Houghton Mifflin Co., Boston.
- ROOT, R. B. 1964. Ecological interactions of the Chestnut-backed Chickadee following a range extension. *Condor*, 66:229-238.
- STEEL, R. G., AND J. H. TORRIE. 1960. *Principles and procedures of statistics*. McGraw-Hill, Toronto.
- STEWART, R. E., and J. W. ALDRICH. 1951. Removal and repopulation of breeding birds in a spruce-fir forest community. *Auk*, 68:471-482.
- TANNER, J. T. 1952. Black-capped and Carolina chickadees in the southern Appalachian Mountains. *Auk*, 69:407-424.

TOMPA, F. S. 1962. Territorial behavior: the main controlling factor of a local Song Sparrow population. *Auk*, 79:687-697.

WATSON, A. 1965. A population study of Ptarmigan (*Lagopus mutus*) in Scotland. *J. Anim. Ecol.*, 34:135-172.

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