ON REGIONAL MOVEMENTS AND BODY WEIGHT OF BLACK-CAPPED CHICKADEES IN WINTER

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AT PIMISI BAY, on the 46th parallel in central Ontario, the return records of banded Black-capped Chickadees (*Parus atricapillus*) suggested considerable movement among the winter populations. Other workers have found this to be true, notably Odum (1941, 1942) and Blake (1952). A connection seemed to exist between the pattern of these movements and the recurring reports in certain years of large concentrations of migrating chickadees south of Pimisi Bay, from the Atlantic coast westward. It occurred to me, therefore, that an investigation might be of interest into the changes in weight and fat deposition of the chickadees and the similarity, if any, of these processes with those taking place in certain true migrants; *e.g.*, the White-throated Sparrow (*Zonotrichia albicollis*) and the Slate-colored Junco (*Junco hyemalis*) as found by Wolfson (1942, 1953, 1954) and Odum (1949). This study was begun in the fall of 1948 and continued during five years until the spring of 1954.

ACKNOWLEDGMENTS

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METHODS

The research was conducted during the winter half-years from August-September to April-May. Efforts were made to handle every chickadee, returns as well as new birds, which frequented the feeding-station. With the exception of the period from October 1953 to March 1954, when opportunity to weigh the birds was lacking, it is possible to say that few of our chickadees escaped being caught each winter.

Often 50 to 60, once 78, chickadees were handled in one day, representing practically all present in the neighborhood at that time. A dab of scarlet nail-polish was applied to the white edgings of the primaries of each chickadee handled. Those that escaped capture showed up plainly. They seldom exceeded half a dozen. The red marking, or traces thereof, endured throughout the season.

At first two Potter's and two automatic trip traps were kept working all the time. However, the birds soon became more and more difficult to re-catch in this way, since they developed either fear of the traps or learned how to avoid tripping them. For this reason all-day trapping sessions were introduced, covering most half-month periods of the six years, during which a minimum of food was made available except in the traps. This worked well taking all considerations into account, such as the varying experience, the difference of individuality, and the rhythm of the daily activities of the birds. Usually the inexperienced new arrivals filled the traps from early morning until well into midday while, the more the afternoon advanced, the greater the number of "repeats" until during the last hour before roosting time even the most stubbornly evasive of the experienced chickadees could be expected to yield a record.

All weighings were done on a Cenco balance to the tenth of a gram. To immobilize the birds paper cones were used. These cones were weighed before, after, and sometimes during a session because the humidity of the air and dirt accumulating influenced their weight. The bird's net weight was recorded. No bird died during the process.

Sex determination.—Three criteria were used to determine sex: 1) wing-length, 2) vocal notes, and 3) behavior.

For obvious reasons only color-banded birds came into the last category.

When being handled certain chickadees often emitted a special protesting cry similar to, if not identical with, the "hissing" sound given by the females when disturbed on the nest. With the exception of 4 birds which were placed in the "undetermined sex" group, none of the chickadees classed as males, with wings measuring 66 mm. and over (see below), gave this note.

All wing measurements were taken from the bend to the tip of the longest primary without flattening the folded wing (Wolfson, *in litt.*). Odum's (1943:178) standards for sex differentiation according to wing-length was followed, *i.e.*, males—66 mm. and over, females—63 mm. and less, undetermined sex—over 63 to 66 mm.

Wing-lengths ranged from 61 to 71 mm.; the average of 573 measurements was 65.8 mm. Many chickadees showed noticeable shortening of their wing-lengths through wear from fall to spring, often as much as one to two millimeters. The average of 285 measurements taken in October, November, December, and January, was one-half millimeter longer than that of 288 taken during February, March, and April.

Fat determination.—The amount of visible subcutaneous fat was also recorded at each weighing. The principal body areas observed were the *abdomen,* usually filling first in the chickadees, the areas around the wish-bone (*furculum*), and under the wing (*axilla*), the last place to fill out except in birds in very heavy fat.

According to the classifications worked out for the Oregon Junco (*Junco oreganus*) and the White-throated Sparrow (Wolfson, 1945:109; 1954:415), the amounts of fat were divided into 4 classes:

1) None—no fat visible or only slight traces in some or all regions;
2) Little—fat seen in area of *furculum* or abdomen, small amounts elsewhere;
3) Medium—*furculum* or abdomen full, puffiness in other regions;
4) Heavy—*furculum* or abdomen overflowing, swollen, other regions full.

The variation of the coloring of the fat in the chickadees was, at first, a puzzling discovery. It ranged from orangy yellow to creamy white. Not until I had seen the hourly variations in weight and fat deposition in a number of chickadees did I realize the apparent reason for this difference. Fat that was in the process of being replenished gradually changed from yellow to white and, conversely, that being depleted from white to yellow. While it was not always possible to determine whether the fat in a particular chickadee was being laid on or lost, the observation was of help sometimes in deducing the probable movements of the bird. For instance, a chickadee with more white than yellow fat might be laying it on prior to departure and this could then be either confirmed by the bird's disappearance or disproved by its next retake.

In all, 1279 weight records were obtained from 340 chickadees of which 113 were males, 154 females, and the sex of 73 could not be determined. Of all these 197 were weighed once or only during one half-year, whereas 143, or 42 per cent, were weighed during more than one season, many of them several times each winter. One female disappeared at 9 years of age after having given 5 records in 8 winters and another gave 19 records in the course of 5 winters.

The Yearly Variations of Winter Populations

With the exception of four species, the Pileated Woodpecker (*Dryocopus pileatus*), the Hairy Woodpecker (*Dendrocopos villosus*), the Great Horned Owl (*Bubo virginianus*), and the Ruffed Grouse (*Bonasa umbellus*), the term permanent resident is applied correctly only to birds of other Pimisi Bay species whose permanency of residence was evidenced by marking.

Most of the Black-capped Chickadees accommodated on the nesting-grounds within about half a mile of the feeding-station proved to be year-round residents. Even among these, certain color-marked birds were not domiciled in the area continuously, but were there one year and gone the next.

If by migration is meant any movement from one area to another, by far the greater part of the chickadees concentrating at Pimisi Bay at one time or another during the winter were migratory. How far they went and how great distances they came from are other questions. None of the over 500 chickadees I banded were retrieved elsewhere. I did not encounter any of these banded birds farther away from the feeding-station than one-half mile, nor were they reported seen at neighboring feeding-stations beyond that distance. Obviously, a considerable number of the chickadees wintering at Pimisi Bay travelled some way to reach this area in which a stable supply of artificial food was to be found, in addition to the natural resources. However, lacking this special supply, doubtless the chickadees would have been even more mobile and dispersed.

So far as I could discover, most of the winter-resident chickadees did not breed in the territory around Pimisi Bay that I could reach on foot beyond the half-mile radius of the feeding-station. On the other hand, wide areas north and east, stretching more than a hundred miles into northern Ontario and across the Ottawa River into Quebec, contained chickadee habitats of the best kind, of which even the closest ranges could well absorb vastly greater numbers of chickadees than appeared yearly at the feeding-station.

Odum (1941:529) described the winter feeding ranges of the Black-capped Chickadees at Rensselaerville, New York, as extending over from 21 to 55 acres, averaging 36 acres, and noted that the birds concentrated around the feeding-stations. Blake (1952:167) observed large numbers of moving chickadees during the winter in Massachusetts. "Even though the distances travelled may be small, I would regard these moving birds as true migrants especially since they are not seen again."

Figure 1 presents an analysis of the number of wintering and transient chickadees based on captures and re-captures during the winters 1948 to 1953 in relation to the approximate mean temperature of the three summer months in these years.

Birds taken within the same month as they were first captured but not again, and those not retaken during the same season are considered transients. Those retaken once or several times during the winter, including those which arrived in January and were re-captured in March, are counted as wintering. A few may, of course, have escaped capture but not in sufficient numbers to alter significantly the picture of the diagram. The winter 1948-49 is not included because the study was not yet fully organized at that time.

During the winters 1949-50, 1950-51, and 1952-53, as can be seen, the chickadee populations maintained fairly constant near-the-peak levels, although the number of wintering chickadees in 1950-51 declined rather sharply. Except in 1950 and 1951, the mean temperatures of the other three summers were high and, significantly, there were no reports of any major movements of chickadees south of Pimisi Bay in the fall and winter following these three summers.

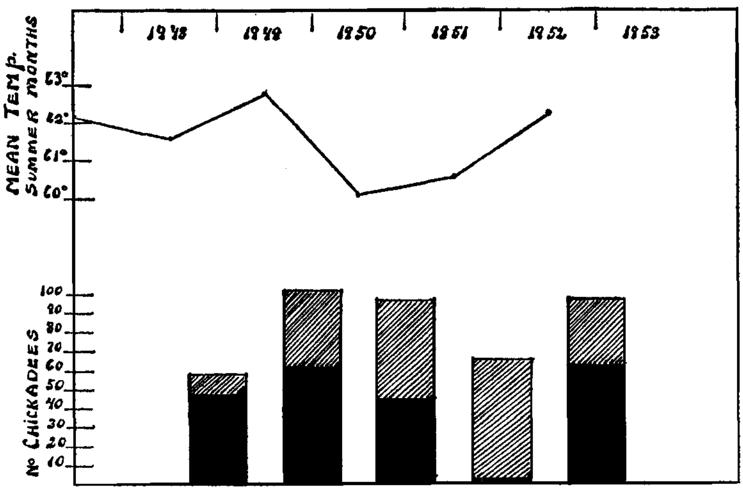

FIGURE 1. The number of wintering and transient chickadees, 1948-1953, in relation to the approximate mean temperature of the three summer months. Black denotes wintering bird; hatching denotes transients.

In the winter of 1951-52, on the contrary, a sharp decline occurred at Pimisi Bay especially in the number of wintering chickadees. During the end of August and the first week of September an unusual influx of chickadees was noted, but they vanished again soon after. During November returning chickadees, chiefly, arrived in rather greater numbers than usual (see next section) and most of these were *not* again retaken in that season. With scattered birds coming and going, and including the spring concentration in March, the average counts of the chickadees throughout that winter remained relatively low.

Without a doubt, these observations at Pimisi Bay stood in close relation to the great incursion of chickadees reported in *Audubon*

Field Notes (1952) from the Hudson-St. Lawrence and Ontario-Western New York regions for the fall of 1951. In his summary for this period Ludlow Griscom (1952:4) said: "Black-capped Chickadees, extraordinary flood through southern Ontario (up to 1400 in a day)."

What caused the spectacular migration in this particular year? It is to be noted that the summer of 1950 was exceptionally sunless and cold and the season of 1951 no less so, with a mean temperature for June, July, and August, less than a full degree higher. Cold and sunless summers affect the numbers and survival of the insects which constitute 68 per cent of the Black-capped Chickadee's food, according to examined stomachs (Odum, 1941, quoting Forbush). Cold also reduces the fruition of the conifers, the seeds of which form another important food item for the chickadee in fall and winter.

However, one cold summer (1950) apparently had not sufficient influence upon the chickadee food situation to necessitate an immediate exodus. Only a slightly greater dispersal of the wintering chickadees ensued, causing a decline in their numbers at Pimisi Bay. The critical period was evidently delayed until the fall of 1951 after another cold summer had followed the first one. This prevented the recovery of the insect life and left the conifers unproductive for another year at the same time as the new generation of chickadees, although apparently not a numerous one (see below), emerged upon the scene. It seems evident that the food factor was the main issue underlying the migration of the chickadees in the fall of 1951.

Lack (1954) maintained that the ultimate reason for the movement and dispersal of birds is the food supply. In this connection reference should also be made to Koskimies' (1955:17) discussion on the influence of the "food limit" upon cyclic and irruptive species, especially in the north.

According to the present study, immediate weather conditions, such as cold spells, appeared to have little bearing on the movements of the chickadees, at least insofar as they were of noticeable proportions. Obviously these hardy little birds could endure severe winter weather without special difficulty, provided they were in good health and able to roost with full stomachs. We shall return presently to the last condition.

Odum (1942:156) found that high temperatures in April when the breeding season started not only increased nesting success but also promoted double broods. In 1941, this apparently created a population pressure in New York State which, he suggested, was an important factor in the irruptive southward migration of Black-capped Chickadees which occurred in the fall of that year.

At Pimisi Bay, however, the spring preceding the cold summer of 1950 was late and cold. Snow still covered the ground on April 23 and the ice went out of the lake at the record late date of May 6. The same was the case in 1951 when snow remained on the ground up to April 20 and northerly winds prevailed almost incessantly from the last of April to May 14.

If an early spring and good weather are significant factors in producing a nesting success high enough to create population pressure, these conditions were entirely lacking at Pimisi Bay both in 1950 and 1951. The late emergence and the small numbers of fledglings recorded in those years indicate a minimum reproductive increase. The migration in the fall of 1951, of which the first signs were recorded at Pimisi Bay (see p. 419), must therefore have been initiated by another factor in these northern regions, *i.e.*, failing food supplies resulting from two successive late springs and cold summers. Only as the great flocks of chickadees reached more southerly parts might actual population pressure have become the chief factor in the further dispersal of the birds.

Monthly Variation in Winter Populations

In the years 1948-54 the total number of returned and newly banded chickadees showed three major peaks in November, January, and March. There was a fourth in September consisting of new birds, probably mostly juveniles.

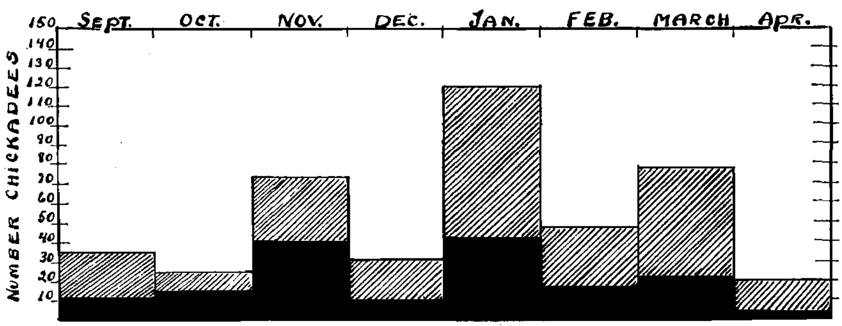

FIGURE 2. Total number of banded chickadees, 1948-1954. Solid black denotes returns; hatching denotes newly banded.

The returned chickadees were most numerous in November and likely this early return to the wintering ground is related to some of these birds being guided by memory back to the previously known locality of the feeding-station. Occasionally two chickadees, originally caught on the same day, would be retaken together in another year, suggesting a certain attachment between some of them beyond the breeding season. Nice (*in litt.*) made the same observation in the Carolina Chickadee (*Parus carolinensis*). Eighteen per cent of the wintering chickadees arrived in November.

When added together, the total number of chickadees for January was higher than in any other month of the half-year, although the influx did not always reach its peak at this time every winter. Apparently a climax dispersal generally occurred in mid-winter. This contention is also supported by the fact that most of the January arrivals were new birds. Forty-five per cent of the chickadees that stayed the rest of the winter came in January.

The March peak represented the chickadees' spring migration back to the breeding-grounds. As might be expected, the new birds were also here in the majority.

In the Toronto area several wintering species, notably the Tree Sparrow (*Spizella arborea*) and the Snow Bunting (*Plectrophenax nivalis*), both of which are true migrants with fall and spring peaks, show this "three-peak-phenomenon" (Speirs, *in litt.*), the mid-winter peak being attributed to the aggregation of large numbers in favorable feeding areas.

Variations in Average Weights

Two main trends emerged in the variations of the average weights of the chickadees—the fluctuations from month to month and those that occurred each day between the awakening hour and roosting time. Both these acted constantly upon the weight of the chickadees and affected that of any individual at any given period or hour.

Owen (1954) carried out an investigation in England into the weights of five species of titmice, chiefly Great Tits (*Parus major*), Blue Tits (*P. caeruleus*), and Coal Tits (*P. ater*), from November to March in 1951–52 and from November to December in 1952 and Haftorn (1951) worked with Great Tits in Norway during the winters 1935–40. Both demonstrated the same two trends in the weight variations of their birds, as did Baldwin and Kendeigh (1938), Nice (1938), and others in many North American species.

The chickadees showed an average difference in weight between the sexes of a little over a gram, the males being heavier than the females. The greatest and smallest male weights were 14.3 and 10.5 gms., female 13.8 and 9.5 gms. Some individuals, irrespective of sex, were constantly much heavier than others.

TABLE 1

AVERAGE WEIGHTS OF THE BLACK-CAPPED CHICKADEES, 1948-1954

Month	*Males* *No weights*	*Average grams*	*Range grams*	*Standard deviation*	*Females* *No weights*	*Average grams*	*Range grams*	*Standard deviation*
Aug.-Sept.	13	12.1±0.08	11.3–12.5	0.30	25	10.9±0.11	10.0–12.0	0.52
Oct.	14	12.0±0.10	11.2–12.5	0.35	23	11.1±0.12	10.3–12.2	0.57
Nov.	43	12.3±0.08	11.3–13.8	0.55	62	11.1±0.11	9.8–12.8	0.91
Dec.	32	12.5±0.10	11.7–13.9	0.60	35	11.3±0.05	10.4–12.6	0.28
Jan.	88	12.6±0.06	10.5–14.0	0.58	128	11.3±0.05	9.5–12.8	0.54
Feb.	60	12.7±0.08	11.8–14.3	0.62	83	11.5±0.08	9.9–13.0	0.71
March	136	12.4±0.05	11.0–14.3	0.61	218	11.4±0.06	9.7–13.8	0.82
April	48	12.4±0.08	11.3–13.9	0.56	79	11.3±0.08	9.7–13.1	0.71
May	1	14.0			6	11.9	10.6–12.8	
	435	12.5	10.5–14.3		656	11.3	9.5–13.8	

The Influence of Migratory Movements

Table 1 shows the average monthly weights for the years 1948–54. Beginning in October, a steady rise in weight ended in a peak in December and was thereafter followed by a slight decline in January and a climax rise again in February. The weights in March and April-May were as high as in January (see Figure 3). In the males the weights rose steadily to the February peak, dropped in March and levelled off in April. In the females the rise to the February peak was less steep and there was a decline in April.

It will be noted that the peaks of the weights show a certain correlation with the times of greatest influx of the chickadees. This became

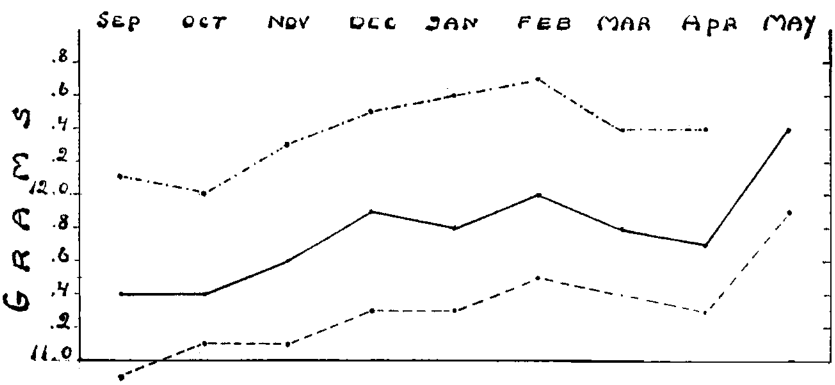

FIGURE 3. The average monthly weights of the males, the females, and the total number chickadees, including those of undetermined sex. Males —·—. Females ————. All birds ————.

still more marked when the weights were computed in half-monthly periods (see Figure 4). The minor movement in September was reflected in the slight increase in weight in the last half of that month and in the first two weeks of October. The November influx was accompanied by weight increases in the last part of that month and in early December. The January peak similarly coincided with increases in weight in the last part of the month and in early February, while the weight increase in the second half of March came just before the spring exodus, which usually took place about that time and in the first part of April.

Wolfson (*in litt.*) expressed the opinion that in an altogether sedentary species the weight variations would be negligible, *i.e.*, the difference between the low weight in the fall and the highest before spring would be small. In the regularly migrating White-throated Sparrow this difference is about 15 per cent (Wolfson, 1954:424).

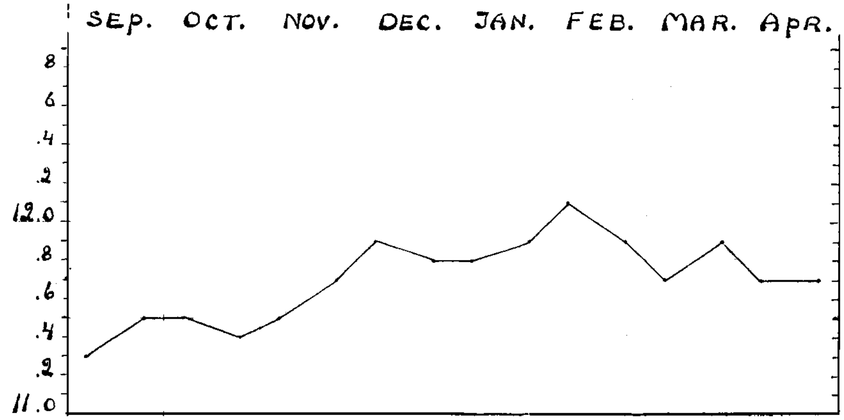

FIGURE 4. The average weights of the chickadees 1948-1954, calculated in half-monthly periods.

This contention led me to analyse the weights of 45 chickadees, 28 of which were residents and 17 non-residents. These birds had been weighed no less than 7 times each throughout one or several seasons and their status was determined by marking and retakes.

The difference between the lowest and highest weights of these birds was calculated in per cent of the low weight and the result is shown in Figure 5. In the non-resident group this difference was over one-third greater than in that of the residents, or an average of 11.1 per cent, ranging from 8 to 17, while it was less than 8 per cent in the

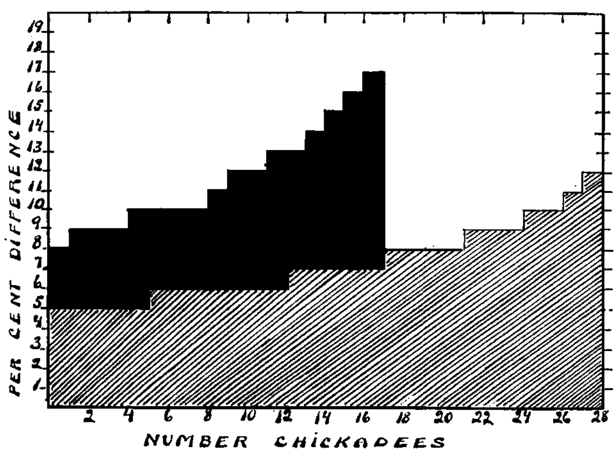

FIGURE 5. The difference between the highest and the lowest weights of 17 transient (solid black) and 28 resident (diagonal hatching) chickadees calculated in per cent for each bird.

majority of the residents, or an average of 7.3 per cent, ranging from 5 to 12. This shows a fluctuation in weight of the non-resident chickadees rather similar to that of the White-throated Sparrow, although not quite as great.

Discussion.—If an increase in weight immediately before a migratory movement and the rebuilding of the body weight during stop-overs occur in true migrants, as in the White-throated Sparrow, Junco, and others, the thought is justified that migrating chickadees also would respond in the same way. In that case their greater fluctuations in weight would influence the average weights of the whole group at critical points, bringing up peaks in weight at or about the time of greatest movement.

As shown in Figure 4, the variations in weight follow too closely the pattern of the chickadees' movements to be dismissed as purely coincidental. It is to be noted that the weight peaks in October, December, and February, occur *after* each of the first three periods of greatest movement, reflecting a majority of *arriving* chickadees rebuilding their body weight at the source of ample food supply. Undoubtedly, more chickadees arrived than departed from a locality where the concentration was marked during the main period of southward movement, extending approximately from September to January. At any rate, the departing chickadees obviously were not numerous enough to produce a pre-migratory increase in weight so great that it influenced the average of all the chickadees together, including both transients and wintering birds. In March, however, the picture was different. The moving birds were northbound, the concentration of chickadees at Pimisi Bay was bent on dispersal, the majority were *departing*. It was to be expected that, if any premigratory increase were to influence the average weight of all the chickadees, not only must it involve a great many birds, but since this particular physiological response usually appears to be very rapid it must happen, not after, but before or during the period of greatest movement. This, indeed, was also the case.

These two data—the difference in weight fluctuation between resident and non-resident chickadees and the correlation found in the patterns of the average monthly weights and movements of the chickadees—constitute the evidence, as far as it goes, demonstrating the influence of migration on the weights of the chickadees. A few instances of confirmative findings may be added, which come to light later in the discussions on the temperature of the air and the fat deposition. While the effect of migration upon the weight fluctuations appears to be negligible, this of course has a reason. In a mixed population of residents and migrants other factors also come into play counteracting this effect, making it far less pronounced than it would be in a group consisting of only regular migrants.

It is strange that neither in Owen's study in England nor in Haftorn's in Norway were any increases found in the average weights of their birds after December. Owen (1954:306) recorded a steady decline from November to March, although his data included records from residents as well as from "immigrants and birds of passage, which groups are likely to reach their peak weights at different times during the winter." Haftorn's birds reached their peak weight in December, followed by a continuous decline until March when the weights levelled off. It is known that migratory movements similar to those of the Black-capped Chickadees in North America occur in the Great and Blue Tits and are particularly pronounced in the Coal Tit, at least in Scandinavia (Särdson and Durango, 1950:236–239). Possibly more extensive data on the European species might alter the picture in this respect.

The Influence of the Temperature of the Air

Owen (1954:304) considered the air temperature an important variable influencing the weights of his birds. The variation in weight shown by three species of his tits during a week in 1951 and the same week in 1952 he attributed to a difference in temperature of 10.6 degrees Fahrenheit. He pointed out that cold spells result in increased feeding and increased weight, but when food is scarce the weight may fall instead. Haftorn (1951:90) found that the mean weights of the Great Tits were relatively low during mild winters, but when the

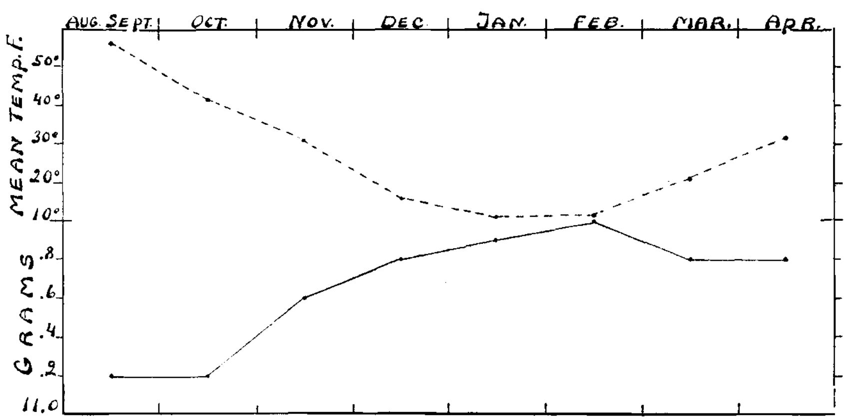

FIGURE 6. The average weights ——— of 66 wintering chickadees in relation to the mean temperature – – – –.

mean temperature decreased the mean weight correspondingly increased.

Baldwin and Kendeigh (1938) conclusively established the inverse correlation between temperature levels and the weights of several species of North American birds.

A test group was selected of 66 chickadees known to have spent the winter uninterruptedly at Pimisi Bay. Their weights (see Figure 6) followed even more closely in inverse order the variations of the mean

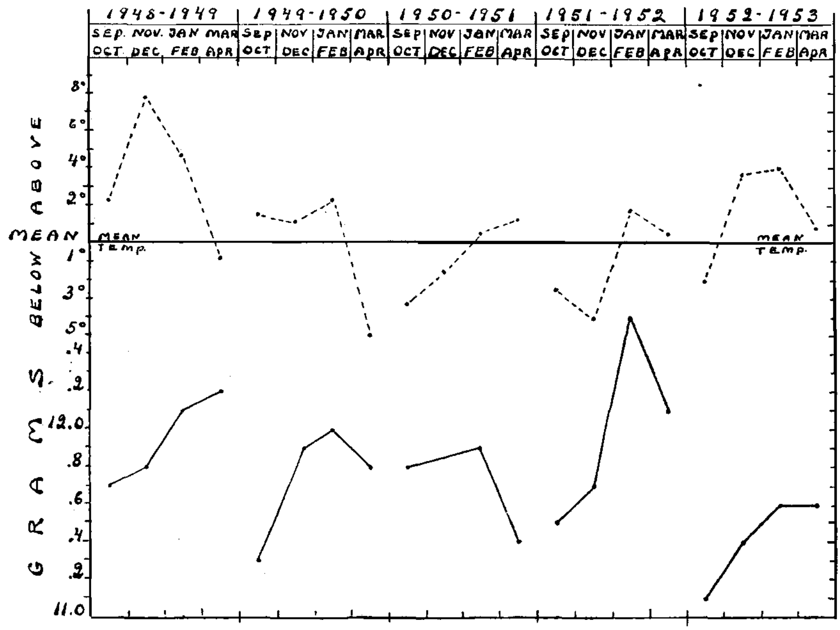

FIGURE 7. The average weights ——— of the chickadees in the winters 1948–1953 in relation to the degrees – – – – above or below the mean temperature Fahrenheit.

monthly temperature than any other group (see Figure 3). The December peak of all the chickadees (center diagram, Figure 3) cannot be said to correspond entirely to the drop in temperature in that month and it must therefore be influenced also by another factor (see discussion on migratory movements). Nor was the levelling off of the weights in March and April-May, shown in all groups except the females, wholly dependent on temperature but influenced by still another factor which I shall discuss later.

When the average weights of the chickadees were calculated for each year separately and compared with the deviations from the normal mean temperature during the same periods the interesting picture of Figure 7 emerged.

First, in the winters 1949–50, 1950–51, and 1952–53, when the weights were 12.0 gms. or lower, the temperatures were not above normal, as would have been expected, but rather the contrary. Only in one year, 1952-53, was the temperature so much above normal that it may, to some degree, have induced the very low weights shown throughout that winter. In the other two winters, 1949–50 and 1950–51, the rather low mean temperature seemingly elicited no response in the chickadees by markedly higher averages of weight. In the fall of 1948 no drop in weight reflected the much above normal temperature of November-December, but the increase in weight in March-April 1949 probably was, at least in part, due to the drop in temperature at that time. The winter of 1951–52 was the critical year when the great migration took place. However, the chickadees did not respond by increases in weight to the unusually cold period in the fall of that year and a food shortage is more likely the factor at work here. Moreover, the unprecedented high peak in January-February certainly cannot be considered in inverse correlation to the above normal temperature, nor does it demonstrate a food shortage and only the factor of migration remains to account for it.

Second, it is to be noted that, irrespective of the vagaries above or below the normal mean of the temperature, all but one winter (1948–49) displayed consistently higher mid-winter levels of weight compared to those of the fall and spring. This pattern of inverse correlation to the mean temperature of the weight curve, corresponding to Baldwin and Kendeigh's (1938:446) principal findings, was shown and followed by the chickadees at Pimisi Bay with remarkable exactitude, when separated into groups or all taken together and apparent even in representative records of the single individual. Thus, by the gradual rise and fall of their average weights the chickadees consistently responded to the gradual fall and rise of the *mean temperature* pertaining to the changing seasons of autumn, winter, and spring.

However, this principal effect of the temperature does not prevent its minor vagaries from being, on occasion, reflected in the variations of weight in birds. Every observer has noticed the increased feeding activity in cold weather, and the influence thereof upon the physiological condition of the bird has been recorded by many workers; Owen (1954) quoted Hicks, 1934, working with Common Starlings (*Sturnus vulgaris*) and Kluijver, 1952, with Great Tits. These variations in weight appear to be connected directly with the food supply and are therefore not wholly temperature-dependent. Thus, as Owen pointed out, if plenty of food is available the birds respond by "overeating" during cold spells, putting on weight and fat reserves; but if an insufficiency of food does not allow "overeating," which is the bird's immediate response to greater heat loss, it grows thin and loses weight.

Haftorn (1951:90) felt that a possible shortage of food was responsible for the continued decline in weight of his Great Tits after December and that therefore January and February, with the lowest temperature of the winter and food perhaps at a premium, were the critical months. This conclusion, it seems to me, would apply only to a stationary population which, after depleting the available food supply to the limit, could move nowhere to relieve conditions (see also Koskimies, 1955:17–18).

Owen (1954:308) ascribed the early peak and subsequent decline in weight of his titmice to an "adaptive process to provide for possible food shortage later, weight being put on when food is still plentiful." If this had been the case with the Pimisi Bay chickadees, their early accumulated fat reserves, being expended steadily in the course of the winter, would scarcely have sufficed to maintain such a high average weight up to and including March as shown in this study. Obviously, the food supply for the chickadees that wintered at Pimisi Bay, as well as for the transients, with the exception perhaps of the fall months in 1951, was generally speaking adequate throughout the five winters in keeping their subcutaneous fat continuously replenished (see section on fat deposition); and when it was not sufficient they did not remain to starve but moved out.

THE INFLUENCE OF OTHER FACTORS

The data show that the weights tended to level off in March, April, and May, at a figure higher than was obtained in the fall months of September and October. The weight for April was 0.1 gm. lower than that for March, while May, taken separately, was 0.5 gm. higher than April.

This levelling off of the weights in spring was also shown in Haftorn's investigation, although his total weight records for the five springs did not exceed 35, and with the difference that it appeared already to begin in February. Baldwin and Kendeigh (1938:434–35) discussed this phenomenon and its causes at some length.

It is logical to think that the incipient breeding cycle would influence the average weights of the chickadees with the growth of the gonads and the levelling off in March and April of the males' weight, as the result of the increasing size of the testes seems evidence of the fact. The females, however, with the full development of the ovaries occurring somewhat later and the exertion of excavating nest cavities, at which they usually work harder than the males, continued to decline in April but showed a significant increase in May. Kluijver's data (1952) show an increase in weight of the female Great Tits in April, but this slight shift in time is probably due to an earlier beginning of the breeding-season in the milder climate of the Netherlands.

The rise in May of the weight of the Pimisi Bay chickadees (Figure 3) requires an explanation. The data were derived from the records of only 7 birds. Four of these were wintering females, one a wintering male, all residents remaining to breed in the area, and the last two were transients, possibly also females. The male was a particularly heavy bird—his mean weight from 7 weighings during two years was 13.7 gms. Since the time of the day when the weighing took place plays an important role, it is of note that all but one of the seven May weights were recorded after 15.00 hours.

If the two unsexed birds are included as females, four of these showed peak weights in May (three of them in six and one in two weighings), the fifth female declined 0.1 gm. from her March weight, and the sixth lacked comparative data as she was weighed only once. The second week of May, when all the weighings except that of the sixth female were done, is within the egg-laying and start of incubation periods of the chickadees nesting at Pimisi Bay. Hence, even after the effect of the heavy male and the late afternoon weighings is discounted, the influence of 4 to 6 egg-heavy females upon the average weight for May can scarcely be ignored.

The conclusion seems justified that the increase in May and the level of the weights in April were at least partly due to the increased size of the sexual organs in most of the birds, to the presence of eggs in the females, and perhaps also to the fact that some birds at the onset of incubation usually maintain a good weight, only slightly lower than during the egg-laying period (von Haartman, 1954:47; own unpublished data).

THE HOURLY FLUCTUATIONS OF THE DAILY WEIGHTS

Several investigators have recorded and discussed the hourly changes in weight in birds. In a Common Redpoll (*Acanthis flammea*) Shaub (1950) found variations in weight up to 15 per cent in a day; Owen (1954) showed that the daily weight rhythm may be related to temperature; Stegeman (1955) found a maximum weight variation of 30 per cent in 24 hours in a migrating White-throated Sparrow in New York State; Nice (1938) recorded daily weight increases in seven species; Baldwin and Kendeigh (1938) concluded that extreme daily weight variations in small birds may vary with differences in the air temperature, amount of feeding, and other activities.

The hourly mean weights of the chickadees are shown in Table 2. These figures are derived from the records of all the chickadees in the five winters. The difference in grams is obtained by subtracting the average of the first five from that of the last five weights of the day in the months August-November when the data were few and the first ten from the last ten in the other five months. The grand difference is the result of the average of the first 50 being subtracted from that of the last 50 weights of the day of the total recorded.

The data for the fall months, August-November, unfortunately were not sufficiently spread over the daylight hours and may not reflect the trends accurately. Such as they are, however, the fluctuations indicate a certain irregularity caused perhaps chiefly by the influence of the temperature. Peak weights at this time came by no means always at the end of the day but often at any moment in the afternoon. The weight pattern in April, when the air grew warmer and conditions approximated those of the fall, strikingly resembled that of August-November, suggesting basically the same causes.

Starting in December, and through February, a change occurred and the hourly weights after an initial drop, usually before 10.00 hours, rose almost without interruption from the forenoon to roosting time, while the difference between early morning and late evening weights increased.

Furthermore, computing the weights of each hour through every month of the winter half-year (for instance, the hour 07.00-08.00 for August through April) produced interesting patterns. The weights in the hours from 07.00 to 11.00 showed the same kind of irregularity as that displayed by the weights of the warmer months, *i.e.,* August-November and April. Thereafter the later the hour of the day the more clearly emerged the same pattern of mid-winter rise in inverse correlation to the mean temperature, as the diagrams of the monthly weights disclose (see Figures 3 and 6).

To check further, the same data were extracted from the 339 records of the 66 wintering chickadees. As would be expected from less quantitative data, these brought out still greater variations and the artificial food supply, always available and plentiful, may have contributed to these wider fluctuations. Nevertheless, they also displayed the comparatively irregular weight pattern of the warmer months and the earlier hours of the day as in the group including the transient chickadees.

The difference between the earliest and the latest weights of the day varied considerably in the two groups. In the group containing all

TABLE 2

THE HOURLY FLUCTUATIONS IN THE AVERAGE DAILY WEIGHTS OF CHICKADEES, 1948–1954

Hour	*Aug. Sept.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*March*	*April May*	*Mean weight*	*Weighings No*
7-8	—	—	—	—	(12.0)	12.2	11.0	11.7	11.3	16
8–9	—	(12.0)	(12.6)	—	11.5	11.6	11.4	11.4	11.8	34
9–10	10.7	11.4	11.4	(12.3)	10.8	11.2	11.3	12.1	11.3	102
10–11	12.0	11.5	11.5	11.2	11.6	11.6	11.6	11.5	11.6	157
11–12	11.3	11.1	11.3	11.7	11.7	11.6	11.6	11.7	11.6	188
12–13	11.4	11.5	11.7	12.0	11.9	12.1	11.9	12.0	11.9	175
13–14	10.9	11.3	12.1	11.8	12.0	12.2	11.9	11.5	11.9	190
14–15	11.3	11.7	11.4	11.8	11.9	12.0	12.0	11.6	11.8	164
15–16	11.8	11.6	12.0	12.1	12.2	12.4	12.1	12.3	12.2	137
16–17	11.3	11.4	11.8	12.2	12.5	12.2	12.4	11.6	12.1	93
17–18	—	—	—	—	(13.3)	13.1	12.5	12.2	12.4	23
Weighings No	45	46	121	78	254	168	417	150		1279
Diff. in grams	.8	.1	.6	.9	1.6	1.2	2.0	.6	1.1	

NOTE: the figures in brackets denote single weights. For further explanation see text.

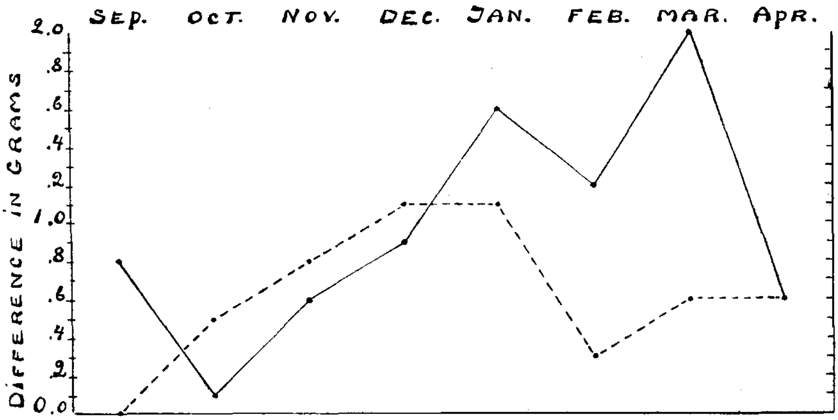

FIGURE 8. The difference in grams of the diurnal variations between the earliest morning and the latest evening weights of all the chickadees ——— and of the 66 winter residents — — — —.

the chickadees, including the transients, it reached almost double the value of that of the wintering chickadees. The last group also lacked the marked peaks in January and March shown by the mixed chickadees, but both groups distinctly displayed the mid-winter rise in this connection as well. The mean difference for the 5 winters was 1.1 gm. or 10 per cent, for the wintering group alone it was 0.7 gm. or 6 per cent.

Discussion.—If great increases in weight occur in many migrating birds during abbreviated periods at certain times, obviously they must also affect the birds' hourly fluctuations in weight at these particular times. Wolfson (1942, 1954a,b) showed how these spectacular increases in weight may occur, and repeatedly pointed out their connection with migration. It is unlikely that even less marked variations in weight of birds belonging to a mixed population of moving and wintering birds, like the chickadees at Pimisi Bay, would not in some manner affect the hourly changes in weight at these special periods. The high peaks in January and March in the difference between the highest and the lowest weights of the day (see Figure 8), which coincided with the major movements of the chickadees in these two months, may well be migration-dependent.

It may be supposed that the food supply of the chickadees was richest in the fall. At this season, spiders were much in evidence and many other insects retiring for the winter into the crevices of twigs and bark became the chickadees' easy prey. The half-opened cones yielded their seeds to the prying bills. Often increased hoarding activity reflected the abundance of food. Judged by the many items one single chickadee could put away within half an hour, the amount of these hidden stores must have been considerable at times. Later, during the chickadees' minute examination of precisely these spots, remembered or not, most of the hoarded food was retrieved—together with that, no doubt, put away by other birds and the squirrels.

During August-November, the need for generating body heat at a high rate was not great because the mean temperature was relatively high and the replacement of expanded energy after a night's roosting less exigent, so that the rise in the daily weight needed be neither spectacular nor regular. The chickadees' visits to the food sources at this time were not only rarer but also shorter. The birds fed with frequent interruptions of various preoccupations related to dominance and other intraspecific behavior. All this may account for the irregular fluctuations of the hourly weights in these months.

Then, in December, although winter had not yet put its seal upon the land, the rise in weight throughout the day increased and stabilized, under the influence of the diminished daylight hours and the mean temperature approaching the winter low. As winter wore on and the mean temperature reached its lowest level in January and February, the chickadees showed accelerated tension in their behavior. For few minutes during the day the feeding-station was empty, the flocks with marked chickadees returning more often, even at noontime and in the early afternoon, when usually the rhythm of their daily activities slowed down temporarily. The tendency to feed reached its height especially in the forenoon and before roosting time. The great speed they developed in pecking and swallowing, the prolonged time they spent at the food sources, the keener competition or unusual tolerance they displayed toward one another according to circumstances, showed this clearly. The chickadees' urgency to feed was exhibited in the quickening of every move. It was evident, certainly, in the relaxed prudence of the old and experienced chickadees during the all-day trapping sessions when in the late afternoons they finally overcame all fear and entered the traps to feed.

The similarity between this accelerated feeding behavior of the chickadees toward the end of the day and that of regularly migrating species toward the moment of departure is striking. My own observations of the Eastern Chipmunk (*Tamias striatus*) and the Striped Skunk (*Mephitis mephitis*) suggest that a parallel exists in hibernating mammals just before retiring. Hunger, meaning the reaction caused by an empty stomach, does not appear to be the direct or sole releaser, since the time when the behavior is at highest intensity coincides rather with a stomach already filling and with fat reserves already being well replenished. To this extent Owen's suggestion of anticipatory feeding seems correct.

The mechanism that controls this behavior is not known, nor do we know if the releasers in the various cases are the same. Baldwin and Kendeigh (1938:460) thought that "the primary stimulus for increased feeding may lie somehow in the loss or in the losing of weight itself, a stimulus which is carried over into the following day." In such a case the effect of the stimulus would be delayed and not anticipatory.

The drop in the early morning weights of birds caught about sunrise or slightly later was characteristic of this period. This was apparently due to the energy expended in the initial foraging during the coldest hour in the twenty-four, while the birds' vital reserves were at the lowest ebb after a long winter's night of fasting. In other words, there seemed to be a time when the intake of food did not register because the requirements of caloric energy were temporarily greater than the supply, and it took a certain time and amount of feeding to get these factors readjusted. Furthermore, the intensive early morning feeding common on milder days was omitted, at least until much later, on days when the temperature dropped lower than 20 degrees below zero Fahrenheit. On these frigid mornings the chickadees (as well as the other birds) were conspicuously absent from the feeding-station. Instead they sought sheltered places exposed to the rising sun. Perched on a twig with all feathers fluffed, they sat facing the sun even on days when its rays did not penetrate the clouds. As protection against the north winds they kept behind them rocks, or the rising ground, or the voluminous branches of dense evergreens. On clear days they perched high up in a tree bathing in sunshine. It seemed as if the acquisition of some warmth from this external source of heat was essential before the chickadees could throw all their effort into feeding on these extremely cold mornings. As the sun rose into the sky, they began moving again and the steady acceleration of their feeding activities, imperative for survival, maintained the rise in weight until roosting time.

This delay in the early morning feeding supported Baldwin and Kendeigh's (1938:461) finding that there is a limit to a bird's capacity of adjusting to extremely cold weather. Nevertheless, the endurance of the northern chickadee, thus temporarily past that limit, appeared highly resilient, for no chickadee in good health and with plenty of food available was found dead at this critical hour or at any other time.

The quick tempo of feeding was more marked on cold than on milder days and it was particularly marked on days preceding a very cold night. Not only was this necessary for keeping up with the increased caloric requirements induced by the cold, but so as to accomplish it, in addition, in a shorter time, because on such days the chickadees emerged later in the mornings and went to roost earlier. Thus the conditioning of the chickadees to a longer fast on colder nights was achieved in advance in a shorter than usual period of time.

It is difficult to see how this reaction could be released by the weight-loss of the previous night (Baldwin and Kendeigh, 1938:460), which could have nothing to do with, for example, a drop in temperature 24 hours later caused by a cold front. Perhaps the stimulus must be sought in the temperature decline itself, in the initial and continued heat-loss within the bird. No doubt wild birds are very sensitive to very slight changes. On many occasions I observed the chickadees go into the fast feeding tempo without any, to me, perceptible indications that the temperature was about to drop below the usual day and night variation, except in the rise of the barometer on my wall and the change of wind direction. Indeed, it may be true that the chickadees can sense also the change of wind and the increasing pressure of the air, even before the temperature starts dropping, without such aids as a weather-vane and an instrument on the wall. However, the internal mechanism regulating these reactions still remains unexplained.

In the marked decline of the difference in morning and evening weights in February, shown by both groups but especially in the wintering chickadees (see Figure 8), additional factors evidently entered into play. A shortage of natural foods may, at this time, have been a contributing agent, although it would be difficult to show a sufficiently great change in conditions from January to February to cause it. Moreover, the trend of the average monthly weights, which showed peaks in February, contradicted the existence of the food factor. Even in the critical winter 1951-52, when a food shortage in the north apparently caused the chickadees' irruptive movements in the south, their weights rose to a high peak in January-February. However, the controlling effect of their migration resulting in an adjustment between the population density and the food supply was in all probability partly responsible for this rise. During February the chickadees began displaying reproductive behavior. Singing, having started in January, became prevalent. Chasing, often in flocks swirling among the trees, gradually grew more frequent and intensive. This disrupted feeding sometimes for long intervals, sufficiently so, perhaps, as to influence the hourly fluctuations but not the major trend of the monthly weights. That the wintering chickadees, of which many were residents, showed the greater decline bears out this argument.

The Deposition of Subcutaneous Fat

The physiological implications involved in the deposition of fat in birds are beyond the scope of the author. Only data derived from what the observer has seen with her naked eye will be presented for what they are worth.

The monthly variations in the deposition of visible subcutaneous fat in the chickadees are shown in Figure 9. The conclusion presents

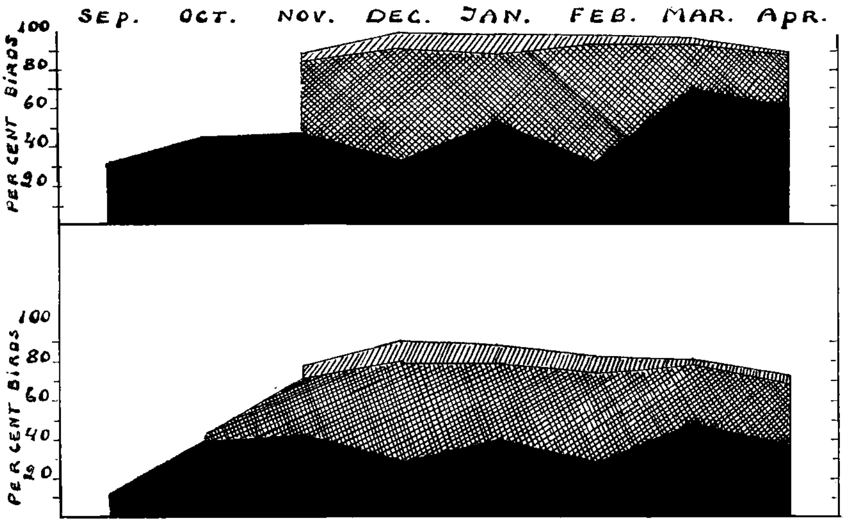

FIGURE 9. Per cent chickadees showing deposition of visible subcutaneous fat. Top—wintering chickadees, bottom—all the chickadees, including the transients. Solid black denotes "little"; cross-hatching, "medium"; diagonal hatching, "heavy."

itself that the accumulation of fat was to an overwhelming degree influenced by the monthly mean temperature.

The peaks in the "little" fat class point of course to a decline in fat at these times and, conversely, the low levels denote an over-all increase as the birds changed from the lower to the higher fat class. The times when these changes occurred coincided precisely with the fluctuations of the monthly weights shown earlier.

However, the similarity between the diagrams representing the accumulation of fat in the two groups of chickadees, with the process underlined in that of the wintering chickadees, indicates a denial of the migration factor and emphasizes the influence of the monthly mean temperature, especially with reference to the highest fat classes. It may be that the showing of the wintering chickadees denotes a latent "preparedness" for migration revealed in the curve of the "little" fat class, but inhibited for lack of enforcement and transformed, as it were, into the greater values of the high fat classes. Individual records (shown below) attest the influence of the migration factor, at least in March. With the passing into the warmer season, the inhibition of fat deposition happened very gradually and the onset of reproductive activities had less drastic effect upon its disappearance than might have been expected.

These findings also furnish strong evidence that lack of food was never a significant factor, even in the dead of winter. Taken in another sense, the regulating mechanism governing the adjustment of popula-

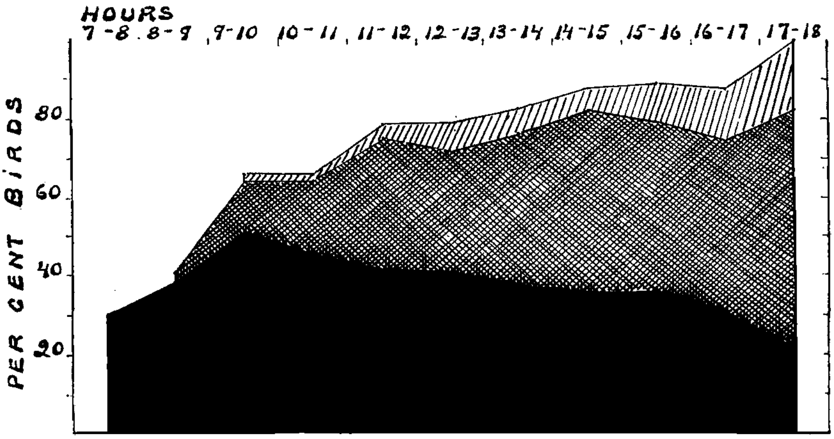

FIGURE 10. The hourly variations of fat deposition in the chickadees. The data include all the birds 1948-1954. Solid black denotes "little"; cross-hatching, "medium"; diagonal hatching, "heavy."

tion density to the food situation was constantly in effective working order. Perhaps the feeding-station was largely responsible for this. Under altogether natural conditions the food situation may play a more incisive role, creating temporary upsets in this important relationship.

As might be expected, the hourly fluctuations in the deposition of fat followed the general outline of the hourly variations in weight (Figure 10). In the individual bird the change from one fat class to another was often spectacular. On some days I could see the fat increasing from hour to hour and puffing out the various regions of the bird's body, its color changing gradually from yellow to creamy white as roosting time approached. A few individual records follow, the data of each bird obtained on the same day.

October records:

Chickadee 22–00246, time 10.10—15.30, increased 0.1 gm., fat class "little," color yellow-white.

Chickadee 22–00253, time 08.50—15.50, decreased 0.1 gm., fat class "none" to "little," color yellow-white.

Chickadee 20–48169, time 09.30—12.45, decreased 0.2 gm., fat class "little," color yellow-white.

March records:

Chickadee 22–00265, time 08.30—14.30, increased 0.5 gm., fat class "little" to "medium," color yellow-white to white.

Chickadee 22–00268, time 09.00—16.10, increased 1.1 gm., fat class "little" to "medium," color white.

Chickadee 22–00259, time 07.30—15.45, increased 1.0 gm., fat class "none" to "little," color yellow to white.

Chickadee 22–00290, time 12.55—13.50, increased 0.4 gm., fat class "none" to "little," color yellow to white.

Chickadee 20–48181, time 10.00—14.45, increased 0.5 gm., fat class "little" to "medium," color yellow to white.

Chickadee 22–00276, time 09.55—17.00, increased 1.3 gm., fat class "little" to "heavy," color white.

Chickadee 20–41878, time 10.20—16.20, increased 1.6 gm., fat class "little" to "heavy," color yellow-white to white.

Chickadee 20–48053, time 09.20—15.20, increased 1.1 gm., fat class "little" to "medium," color yellow to white.

Chickadee 22–00280, time 10.20—15.30, increased 1.0 gm., fat class "none" to "little," color yellow to white.

April records:

Chickadee 20–48189, time 08.40—14.30, increased 0.5 gm., fat class "none" to "little," color yellow-white.

Chickadee 20–48196, time 10.00—17.50, increased 0.4 gm., fat class "none" to "medium," color white.

The October records showed only small and irregular variations conforming to the character of the month (mild autumn weather) and no major movements of the chickadees (compare the monthly and hourly weight variations).

March featured the spring exodus to the breeding-grounds and the fluctuations accordingly were much greater. Of the 25 chickadees yielding adequate morning and afternoon records, 9 of which are given, 3 were residents and 22 transients. One resident showed no change, the second increased 0.3 gm. in weight and the third 0.5 gm., with correspondingly small changes in fat. One transient registered no change in weight but an increase in fat and the remainder increased from 0.3 to 1.6 gm., averaging 0.8 gm., with correlated changes in fat deposition.

The two April chickadees increased 0.5 and 0.4 gm. and the last one, a transient, increased its fat from "none" to "medium"-plus in the course of seven hours.

Although these individual records point to the influence of the migration factor, nevertheless the principal agent acting upon the deposition of fat in the chickadees at Pimisi Bay was the same as the one which most consistently regulated the monthly and hourly weight variations, namely the gradual rise and fall of the mean temperature of the air.

SUMMARY

From the fall of 1948 to the spring of 1954, during the winter half-year August-September through May, 340 Black-capped Chickadees concentrating at a feeding-station at Pimisi Bay in central Ontario were captured, marked, weighed and released. They yielded a total of 1279 weight records, on which this study is based.

Of these chickadees, 113 were considered males, 154 females, and 73 of undetermined sex. Sexing was based on wing-length, on the "hissing" note sometimes emitted by the females, and on behavior. One female yielded 19 weight records in 5 years and another 5, before she disappeared at the age of 9 years. Thirty-two per cent of the chickadees banded from 1942 to 1954 returned, but none was recovered elsewhere.

The majority of the chickadees were migratory in the sense that they came from other places at various distances from Pimisi Bay, some remaining for the winter, others passing on after stop-overs varying in length.

The number of chickadees captured and retaken from year to year was comparatively stable, except in the winter 1951-52. In that year a sharp drop in numbers occurred, involving especially the wintering birds. This coincided with a mass incursion of the Black-capped Chickadees observed in the southern and eastern parts of Ontario, southeastern Quebec, and into the northern states. Two unusually cold and cloudy summers preceded this event, apparently causing an acute food shortage in the northern ranges of the chickadees.

The aggregation of chickadees in the Pimisi Bay area showed four peaks in September, November, January, and March, of which the last three were of major proportions.

The factor most consistently influencing the variations in weight and fat deposition in the chickadees was the seasonal rise and fall of the mean temperature of the air. The influence of temporary cold or warm spells was much less consistent and often counteracted by other factors, such as migration, reproduction, and the food supply. The

accumulation of fat in the greatest number of chickadees occurred in December and their highest weights were recorded in February.

Increases in weight and fat were brought about chiefly by accelerated feeding. Feeding was markedly intensified during the colder seasons and on colder days. Two peaks occurred in the feeding activities during the day, one in the morning or forenoon which halted the weight loss incurred during the night and the other in the late afternoon when maximum weight and accumulation of fat were achieved before roosting time. When the early morning temperature dropped far below zero (Fahrenheit), the chickadees temporarily lost their ability to adjust to the energy drain of the excessively cold weather by an adequate feeding response, but this condition of maladjustment was never known to become so critical as to cause death, except in the case of sick or otherwise impaired birds.

The intimate interplay between the different factors influencing the changes in weight and fat of the chickadees is shown in this study. Any factor, even the most important, seldom maintained its modifying influence undisturbed for any length of time before another began exercising its counteracting pressure.

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