

VARIATIONS IN THE WEIGHT OF BIRDS¹

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INTRODUCTION

IN spite of the fact that the weight of birds may be easily obtained, there is very little information available for wild species. Very few collectors in the past have taken the trouble to weigh the birds that they obtain for taxonomic purposes. One reason for this may lie in the lack of a suitable portable weighing instrument. A more important reason why the weighing of birds has not been more commonly done may lie in the recognized variability of bird weights and the consequent lack of appreciation of their importance. Yet the weight of birds and the variations and fluctuations of these weights furnish criteria of considerable importance in the understanding of the physiological and ecological reactions of the bird as a living organism. The physiology of the bird, its behavior, and the influence of environment are interacting factors, no one of which can be understood without a knowledge of the two others. The weighing of all birds collected might well be made a fundamental policy in all museums. There is a developing tendency to do so among some of the younger ornithologists. A good accurate balance may be obtained at a very reasonable price. Bird-banding operators have an especially good opportunity for obtaining weights of living birds of many species and also of the same individual bird at frequent intervals.

At the Baldwin Bird Research Laboratory, Gates Mills, near Cleveland, Ohio, the first weights of birds were obtained in 1925, and in 1926 the weighing of all birds taken from the banding traps became an established practice in the laboratory routine. The present paper is an analytical summary of the data obtained during the nine years up to January 1, 1934, in the course of which 13,546 weights were obtained of 5812 individuals representing eighty-five species. More than ten individuals were weighed in each of thirty-three species, and these receive major consideration in this report.

Acknowledgment is made of aid from the following persons who, as assistants in the laboratory during various periods, have been of much help in gathering these records: Rudyerd Boulton, W. W. Bowen, Leonard G. Worley, Delos E. Johnson, Carl Johnson, James Stevenson, Theodore C. Kramer, and Roscoe W. Franks. We wish to make special acknowledgment to Dr. Worley who was actively interested in this line of work while at the laboratory and made a useful preliminary summary of the first four years' data.

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LITERATURE

No attempt is here made to review in an exhaustive manner all the literature on bird weights. Attention is centered not on the average and extreme weights of individual species, but on analysis of the variations in the weight of individuals and species under different circumstances. Data on the weight of various species have been recently obtained or compiled from the literature by Krohn (1915), Bergtold (1917, 1926), Hesse (1921), Heinroth (1922), Przibram (1922), Weigold (1926), Whittle and Whittle (1926), Esten (1931), Roberts (1932), Groebbels (1932), Fiora (1933-34), Wetherbee (1934), Marples (1935), Mountfort (1935), Stewart (1937), Imler (1937) and Nice (1938). Several of these authors, as well as Knappen (1928), give useful bibliographies relative to the weights of birds.

Some authors are content with giving single or average weights, with or without indication of the limits of variation. In some cases, distinctions in weight between the two sexes or between adult and immature birds are made, but seldom is any extensive analysis given. Those in the above list who have obtained weights of living birds taken from banding traps are Whittle and Whittle (1926), Wetherbee (1934), Marples (1935), Mountfort (1935), Stewart (1937), Imler (1937) and Nice (1938). Most students, especially those who have weighed living birds and often the same individual at different times, are impressed with the great variability in their weights. Groebbels (1932) finds this variability relatively greater in small than in large birds. Linsdale and Sumner (1934) adequately emphasize this variability in their statement that the "weight of a bird is not a static quality but is one of continuous and ordered change." Other literature dealing with specific problems will be considered in the various sections that follow.

METHODS

Practically all the weights entering into the present study were obtained from living birds; a very few were obtained from birds collected for other investigations. All the living birds were gathered, at intervals of two or three hours, from the banding traps scattered over the fifteen or more acres immediately surrounding the laboratory. They were brought to the laboratory in small gathering cages and weighed immediately. All the birds had thus been recently feeding and had a varying amount of food undergoing digestion in their alimentary tract. Differences in activity and diet previous to entering the traps may have influenced the weights obtained, but these were beyond control.

According to Stevenson (1933), the amount of food in the stomachs of twenty-five adult Song Sparrows,¹ English Sparrows, Starlings, and White-

¹ Scientific names of species are given in Table 5, page 436.

breasted Nuthatches averaged about 1.5 per cent of the body weight. If as much is in the small intestine and a similar amount is in the large intestine and cloaca, about 4.5 per cent of the body weight may represent unassimilated material. Single excrement droppings in these small birds average less than 0.5 per cent of the body weight. A correction of this amount (plus an allowance of about 0.5 per cent for weight of the band on the bird) may be made, if desired, to give the approximate basic weights of the birds. This correction has not been made in the present study because of a desire to follow the natural weight fluctuations of birds in the wild.

The bird for weighing was placed in a rectangular aluminum box (5 by 3 by 3.5 inches) with a loosely fitting cover. As the bird was here in darkness it generally remained quiet, and there was no danger of suffocation. Weights were taken on a small Cenco balance. The box was accurately counterbalanced by means of No. 12 shot, so that the weight of the bird could be read directly without subtracting the weight of the box. The counterbalancing of the box was performed before each weighing because of gradual accumulation of excrement voided by the birds while in the box. The bird was banded and examined before the weighing was done, so that by removing the cover from the box, it could at once be released without further handling. The bird was not in any way harmed by the procedure and often returned to the traps several times a day. The weights of wet or obviously sick birds were not included with the other data. A largely negligible loss in weight of the birds may have occurred from time of removal from the traps until the weight was taken. A careful calibration and checking of the balance and weights indicated in weighing up to 20 grams, an accuracy of ± 0.1 gram, and between 20 and 200 grams an accuracy of ± 0.2 to 0.3 gram. Since much of the following discussion is based on weight averages, many of these small plus and minus inaccuracies in individual weights are largely eliminated.

Since weights of all birds are included in this study, although some individuals were weighed only once and others many times, a special study was made of the effect of the 'trap habit' on fluctuations in weight. It might be expected that where a bird comes repeatedly to the traps and thus obtains much of its food, there would be an interference in the weight physiology of the bird. Adult Chipping Sparrows were used to study this point because only in this species were there sufficient records for a single month (May) between the hours of 8.30 a.m. and 5.30 p.m. free of the influence of age and sex (see beyond).

Table 1 shows an increased amount of fluctuation in the weight of an individual, as represented by the average standard deviation, with an increased number of times it repeats in the traps. This increase, at least the extreme value, is of fairly high statistical significance. However, this in-

TABLE 1

Variability in weight of adult Chipping Sparrows correlated with number of times captured and weighed; there is no sex difference in weight of this species

Number of times bird weighed	Number of birds	Average weight in grams	Average standard deviation, grams ¹
2- 6	30	12.4	±0.40
7-10	24	12.4	0.50
11-20	15	12.2	0.54
21-	4	12.2	0.63

creased fluctuation in weight seems not to be due to any influence of the trap habit in itself but rather to the longer period of time necessarily covered during which the bird is subjected to a larger number of influencing factors. Another reason for believing that the trap habit has no intrinsic effect is that the average weight of the birds is nearly the same regardless of the number of times they were caught. The difference of 0.2 grams is not statistically significant. In the case of a very few individual birds of other species, notably the Cowbird, and occasionally a Song Sparrow, a persistent trap habit did show a positive effect, in being associated with a considerable loss of weight. Such records were eliminated from the averages given in this paper. In most instances the number of records obtained from individuals that did not acquire the trap habit greatly outnumbers those that did, and so no correction or further consideration of the trap habit will be made.

In developing a method for analyzing the weight data, the importance of variations between individuals had to be considered. Here again it was most convenient to work with the data on adult Chipping Sparrows. The average weight of each of forty-three individuals was obtained. All individuals had more than six weights and these were all taken between the hours of 8.30 a.m. and 5.30 p.m., during the month of May for various years. The standard deviation of the weight records around the mean weight of each individual was computed in order to determine the amount of fluctuation that occurred in the weight of each individual bird. The average of these standard deviations for all individuals was ± 0.53 grams, with the extreme values ± 0.15 and ± 0.94 grams. The grand average weight of all the individuals was 12.3 grams. There is no sex difference in weight in this species. The standard deviation of the average weights of individuals from this grand average was ± 0.63 grams. The difference of 0.10 grams in the two standard deviations is small and not greatly significant. The information indicates that differences in weight between individuals may occur,

¹ The standard deviation includes within its limits 68 per cent of all random fluctuations in weight around the true average. According to the law of variability, if an indefinite number of weights were obtained, where the average weight with its standard deviation is 12.4 ± 0.40 , 68 per cent should fall within the range 12.0-12.8. Differences in size of the standard deviation are thus a measure of variation of values around an average.

but it is suspected that if all conflicting factors, as time of day, stage of reproductive activity, recent time of feeding and defecation, weather, and other factors were rigidly eliminated, these individual differences would be smaller even than here indicated. As it is, the conclusion is warranted that differences between the average weights of different individuals are very little if any greater than differences in the weight of the same individual at different times.

The next step was to average, without regard to the individual, all the records (525) upon which these individual averages were based, i.e., each record was given equal value with every other record whether it was one of thirty or more of the same individual or only one of seven. This gave an average of 12.3 ± 0.87 grams (coefficient of variability—7.1). The average is the same as the grand average of the weights of the separate individuals, although the standard deviation is significantly higher by ± 0.24 grams. This means that random weights may be obtained that are higher or lower than the average weight of any individual bird. Comparing this standard deviation with the average standard deviation in the weights of individual birds (± 0.53 grams, coefficient of variability—4.3) shows also that the possible fluctuation between weights within the species is greater than it is in the case of the average individual. The difference between their coefficients of variability shows the same thing. In an occasional individual, however, the standard deviation of single weights around the mean for that individual may be greater, as witness the standard deviation of ± 0.94 above mentioned.

Another factor involved in the extent to which a bird's weight may fluctuate is the relation of an individual's mean weight to the mean weight of the species. This is shown in Table 2 using the same data as above.

TABLE 2
*Extent of weight fluctuations in individual adult Chipping Sparrows of
different average weights*

Range of average weights in grams	Number of birds	Average standard deviation, grams
11.0–11.4	4	± 0.64
11.5–11.9	8	0.52
12.0–12.4	10	0.46
12.5–12.9	15	0.52
13.0–14.1	6	0.52

Since the average weight of the species here considered is 12.3 grams, the data in Table 2 show that an individual varies least in weight when its average weight most nearly agrees with the average of the species. However, the greatest difference in standard deviations is only ± 0.18 grams and this is not statistically very significant. The difference of ± 0.06 is almost

negligible. After taking these various factors into consideration, particularly that the individual may vary in weight at different times and under different circumstances almost as much as the species taken as a whole, it was decided not to put major stress upon individual differences in the compilation and analysis of the data, but to analyze the records of weights irrespective of the individuals on which they were obtained.

The species are listed in the tables that follow in the order of the abundance and reliability of the data for each. Some species are listed in these tables for the sake of completeness although the number of data in their cases are too few to support any generalizations by themselves. When taken in conjunction with the more numerous data for the other species, they have a suggestive significance.

The identification of all banded birds as to sex and age is obviously of great importance in any study such as this. However, this was not actually done in many instances because of the inexperience of the assistant or of apparent difficulties in so doing. A very useful and convenient means for distinguishing the sexes in the House Wren, sparrows, flycatchers, and other species in which the male and female are similarly colored and where it is certain that only the female incubates, is the absence of down feathers in the ventral apteria of the female. This character is useful only during the breeding season. Many individuals were caught in both the breeding and the non-breeding months, so that after having once been sexed during the breeding season, differences could thus be followed into the non-breeding months. Differences in age, i.e., whether adult or juvenal, were determined by differences in markings, in coloration, and in texture of feathers. Juvenal birds also commonly have a yellow pigmentation at the inner angles of the bill that is rather conspicuous. By using one or more of these various methods, most juvenals could be distinguished from adults. When there was any doubt as to sex or age, such records are not included in the averages.

SEX DIFFERENCES IN WEIGHT

The first item in the analysis of the weight data was the study of sex differences (Table 3). All records are included regardless of the number obtained from the same individual. Records are included for all hours of the day regardless of the hourly differences in weight, since the weights were fairly well distributed throughout the day. All records are averaged separately for each month in which data are available for both sexes of a species and then a grand average is made of these monthly averages. This was to allow for possible monthly variations in weight. After a careful examination of the data, an arbitrary limit of 3.0 per cent of the male's weight was selected as representing the lowest amount of difference between the weight of the sexes that could be considered significant. A study of

Table 3 shows that, in nearly all instances, the two sexes weigh either approximately the same or the male is the heavier. In four species the female weighs significantly more than does the male.

When a larger number of records is obtained, the sex differences noted for some of these species may not be substantiated. Stewart (1937) and Nice (1938) found very little difference in the weight of male and female Bob-whites. Wetherbee (1934) found that male Towhees weighed 6.4 per cent more than females but on the basis of only fourteen weights. She verifies our finding that female House Wrens are heavier than the males but found no significant difference between sexes of the Robin. Her female Goldfinches weighed slightly more than the males. Nice (1938) agrees with our sex difference of weight in the Robin in the spring, but finds male

TABLE 3
Sex Differences in Weight of Adult Birds

Species	Months	Male		Female		
		Records per month	Average weight grams	Records per month	Average weight grams	Percentage different from male
<i>Group A—Males and females of approximately same weight</i>						
Chipping Sparrow	4, 5, 6, 7, 8, 9	111	12.3	82	12.0	- 2.4
Field Sparrow	4, 5, 8	26	12.7	4	12.7	0.0
English Sparrow	1, 2, 3, 4, 6, 7, 8, 9, 10, 12	9	27.7	8	28.1	+ 1.4
Downy Woodpecker	1, 2, 3, 4, 5, 6, 7, 8, 9	8	27.2	7	27.2	0.0
Towhee	3, 4, 5, 7, 8, 9, 10	8	41.7	7	40.9	- 1.9
Cardinal	1, 3, 4, 5, 6, 7, 8, 9, 10, 11	6	43.5	3	43.1	- 0.1
White-breasted Nuthatch	2, 3, 4, 5, 6, 7, 8	3	21.3	4	21.0	- 1.4
Bluebird	6	2	30.2	2	29.6	- 2.0
Red-eyed Vireo	5, 8	1	16.0	1	15.6	- 2.5
<i>Group B—Males significantly heavier than females</i>						
Song Sparrow	4, 5, 6, 7, 8, 9	81	21.3	46	20.5	- 3.8
Slate-colored Junco	4	54	21.4	63	19.9	- 7.0
Cowbird	4, 5, 6, 7	8	46.4	18	38.7	-16.6
Brown Thrasher	5, 6, 7	4	69.9	18	66.5	- 4.9
Mourning Dove	5, 6, 7, 8, 9	10	139.6	4	131.8	- 5.6
Black-capped Chickadee	1, 4, 5, 6, 8	3	11.5	3	10.3	-10.4
Hairy Woodpecker	4, 5, 6	3	69.0	2	60.0	-13.0
Goldfinch	7, 8	2	13.0	3	12.6	- 3.1
Bronzed Grackle	4	2	129.0	2	98.9	-23.3
Flicker	6	2	137.6	2	131.0	- 4.8
Starling	3, 5, 6, 12	1	81.2	2	77.8	- 4.2
<i>Group C—Females significantly heavier than males</i>						
Catbird	5, 6, 7	23	34.1	34	36.5	+ 7.0
House Wren	5, 6, 7, 8	29	10.8	16	11.4	+ 5.6
Bob-white	5, 6, 7, 8	4	174.2	2	186.8	+ 7.2
Robin	4, 5, 8, 10	2	73.9	2	79.4	+ 7.4

Cardinals to be heavier than females. These authors' data are not strictly comparable to ours, as they did not consider monthly differences in comparing the weights of the two sexes, but nevertheless more data are required for many of these species.

AGE DIFFERENCES IN WEIGHT

The data showing the age differences in the weight of birds were compiled in a similar manner as in showing the sex differences of the adults. Averages were made for adults and immatures only for those months when

TABLE 4
Age Differences in the Weight of Birds

Species	Months	Adult		Immature					
		Records per month	Average weight grams	Records per month	Average weight grams	Percentage different from adults			
<i>Group A—Both sexes of adults and immatures of approximately same weight</i>									
Chipping Sparrow	6, 7, 8, 9	114	12.1	113	12.0	- 0.8			
Downy Woodpecker	7, 8	18	25.7	10	25.4	- 1.2			
Cardinal	7, 8, 9	8	40.3	10	40.9	+ 1.5			
<i>Group B—Adult sexes the same and immatures less in weight</i>									
White-throated Sparrow ¹	10	151	26.3	233	25.5	- 3.0			
White-crowned Sparrow ¹	10	128	29.7	93	28.6	- 3.7			
Field Sparrow	8	14	13.1	113	12.4	- 5.5			
English Sparrow	6, 7, 8, 9	8	27.5	118	26.6	- 3.3			
Slate-colored Junco ¹	10	27	20.0	14	18.4	- 8.0			
Towhee	7, 8, 9	18	40.5	22	38.4	- 5.2			
White-breasted Nuthatch	6, 7	8	21.0	5	19.4	- 7.6			
Species	Months	Adult Male		Adult Female		Immature			
		Rec. per mo.	Avg. weight grams	Rec. per mo.	Avg. weight grams	Rec. per mo.	Avg. weight grams	% different from adult	
<i>Group C—Sexes of adults differ and immatures of less weight</i>									
Song Sparrow	6, 7, 8, 9	50	21.4	39	20.4	576	19.8	- 7.5	- 2.9
Cowbird	6, 7	5	46.4	20	39.4	124	37.6	-19.0	- 4.6
House Wren	7, 8	27	10.8	11	11.3	26	10.2	- 5.6	- 9.3
Brown Thrasher	6, 7	3	68.4	18	65.0	26	61.6	- 9.9	- 5.2
Mourning Dove	6, 7, 8, 9	10	137.7	4	130.0	9	103.4	-24.9	-20.5
Flicker	6	2	137.6	2	131.0	1	75.2	-45.3	-42.6
Robin	8	1	73.1	1	80.0	2	71.2	- 2.6	-11.0
<i>Group D—Sexes of adults differ and immatures of greater weight</i>									
Catbird	6, 7	23	33.4	30	35.5	40	36.7	+ 9.9	+ 3.4

¹ Adult sexes not distinguished.

sufficient records of both were available. The monthly averages were then in turn averaged to give the figures in Table 4. Immature birds are considered to be those that have left the nest and are living more or less independently of their parents. No study is here made of the weight increase during the growth period of young birds in the nest.

In nearly all instances immature birds weigh less than do the adults. Even in the Catbird where the data indicate that during June and July the immatures weigh more than the adults, some further information (Table 5) shows that during August and September the immatures weigh less than the adults at that time. Wetherbee (1934) also found immature Catbirds during the latter half of July and during August to weigh less than the adults. Her immature Chipping Sparrows, on the other hand, weighed 4.3 per cent less than the adults and her immature and adult Field Sparrows weighed nearly the same, results that do not harmonize with ours. She and also Stewart (1937) found immature and adult White-throated Sparrows to weigh practically the same. Stewart also found immature Chipping Sparrows to weigh 3.5 per cent less than the adults, while immature Field Sparrows weighed 6.0 per cent more. This lack of consistency in results may indicate either a faulty method of analysis or an inadequate amount of data, or both.

HOURLY VARIATION IN WEIGHT

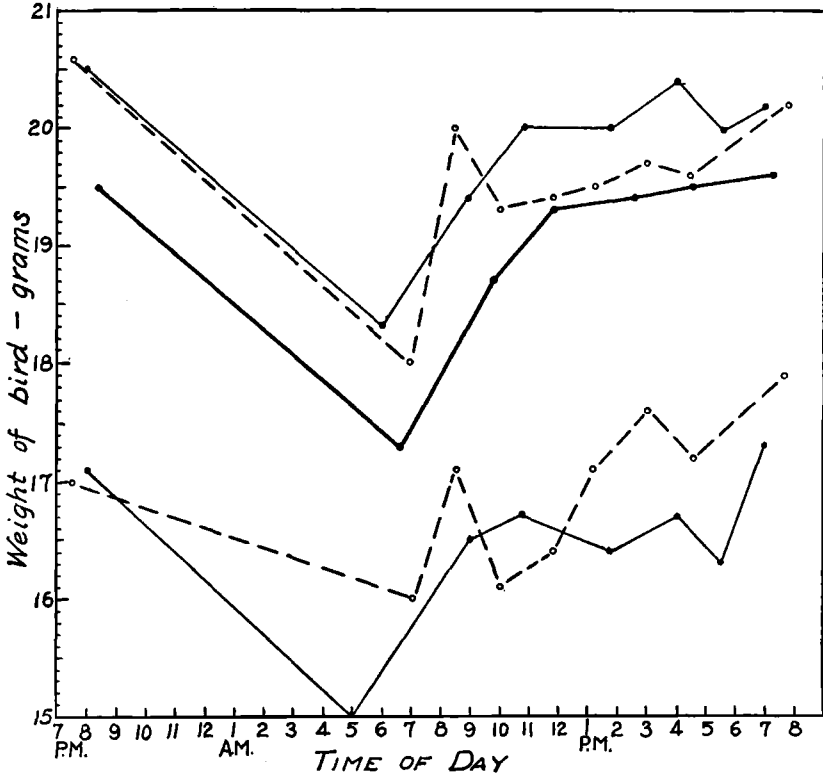
That birds vary in their weight at different hours of the day has long been supposed, although actual quantitative study of such variation is not great. Taber (1928) and Nice (1929) determined that Mourning Doves lost in weight during twelve hours at night an amount equal to between 8 and 9 per cent of their early-morning weight, and Taber found for miscellaneous records of fifteen species this loss to average 7.7 per cent. Weight lost at night must be regained during the day, so this represents a method of determining maximum daily weight fluctuations.

Sumner (1935) determined that the California Quail (*Lophortyx californica*) lost between 6.2 and 9.8 per cent under similar conditions. Stewart (1937) states that an overnight weight loss of about 10 per cent is sustained in the smaller birds but this becomes less in larger birds, being 5 per cent in the Bob-white. Kendeigh (1934) studied weight losses of birds in darkness without food and noted considerable effect of activity, temperature, light, relative humidity, wind, season, and other influences. During twelve hours at an air temperature of 70° F. (21.1° C.), English Sparrows lost approximately 10 per cent and House Wrens 14 per cent of their initial weight.

Partin (1933) obtained over a thousand weights of 800 House Finches (*Carpodacus mexicanus frontalis*) throughout the year. These, when summarized, show an increase in weight during the day and the maximum

reached sometime during the afternoon. The average daily increase in adults he states to be 3.5 per cent and in immatures 5.0 per cent, but minimum morning weights before feeding were not obtained.

Linsdale and Sumner (1934a) studied hourly variations during the day in the weight of Golden-crowned Sparrows (*Zonotrichia coronata*) and found that birds of this species tend to be heaviest in late afternoon, but almost as often reach their greatest daily weight about midday. The birds



TEXT-FIG. 1.—Fluctuations in weight of immature Song Sparrows kept overnight in small cages and given food after first weighing the following day.

increased about 4 per cent in weight from 8.00 o'clock a.m. to 6 o'clock p.m. Other studies by these authors (1934b, 1937) show similar variations in Fox Sparrows and Spotted Towhees (*Pipilo maculatus falcifer*).

In a study of 730 weights of Song Sparrows, Mrs. Nice (1937) also finds that an increase in weight takes place in both male and female toward noon and especially during late afternoon, amounting to somewhat less than 5 per cent. In a study of other species, she (1938) found daily weight

increases up to 10.8 per cent. Stewart (1937) finds a morning to evening rise in weight but with a slight mid-day smoothing or even slumping in the curve of increase.

The hourly variation in the weight of birds during the 24-hour day was studied in the present investigation under both controlled and natural conditions. Text-fig. 1 shows the variation in the weight of captive juvenal Song Sparrows kept in small cages without food overnight and given food after their first weighing in the morning. Only birds were used that were caught in the late evening at the banding traps, so as to have a normal weight with which to begin the experiment. Only five of the more typical records are here shown as some of the other birds experimented with were frightened by the procedure so as not to consume food in a normal fashion during the following day or to increase normally in weight. Experiments with individual birds thus held in confinement were considered successful when the bird's weight on the following day approached, equalled, or surpassed the weight of the bird the preceding evening.

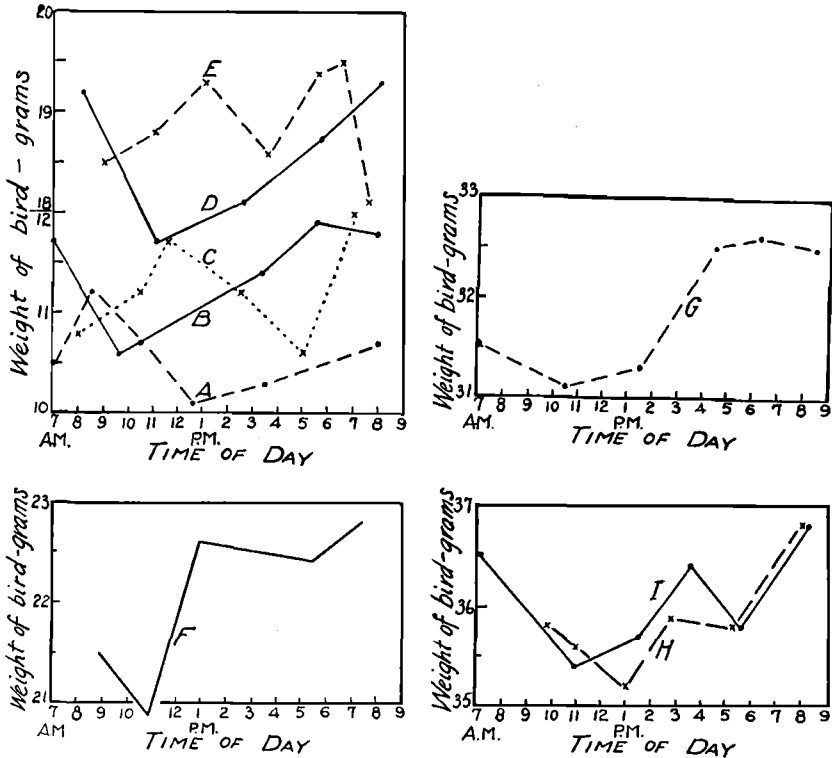
As would be expected, all birds lost weight at night and gained weight the following day. The loss at night averaged 1.9 grams, which is 10.0 per cent of the maximum evening weight and represents a loss overnight of 0.95 per cent per hour (or on the basis of mean daylight weight the night's loss was 10.3 per cent or 0.98 per cent per hour).

The gain in weight during the day shows a tendency to be more rapid during the early morning hours, to become more gradual during the afternoon, and to show a further acceleration, at least in some cases, in the evening. The average maximum increase in weight in these records is 2.2 grams or 11.9 per cent of the mean daylight weight of the birds. This took place in a little more than twelve hours or at the rate of approximately 0.95 per cent per hour.

The daily weight curves of individual birds in a free natural state are similar to those of individual birds in captivity except that the very low early-morning weights, which would occur around 5.00 a.m., were not obtained. In Text-fig. 2 a few of these curves are shown for individuals that repeated in the traps several times during the same day. The tendency is for the heavier weights to occur in the afternoon, but there is considerable fluctuation from hour to hour. Several records show a drop in weight toward the middle of the day.

In order to ascertain the general trend in variations of weight during the day of the bird population as a whole, averages of all weights each hour were computed for each species, age, and month during the summer. No distinction was here made between sexes since both males and females possessed a daily rhythm and records on both sexes were fairly evenly distributed. The weight of the adult birds each hour was then put into terms of per-

centage of the mean daylight weight of the species and all species were averaged together, combining the three summer months of June, July and August, to give the smoothed curve shown in Text-fig. 3. Species entering

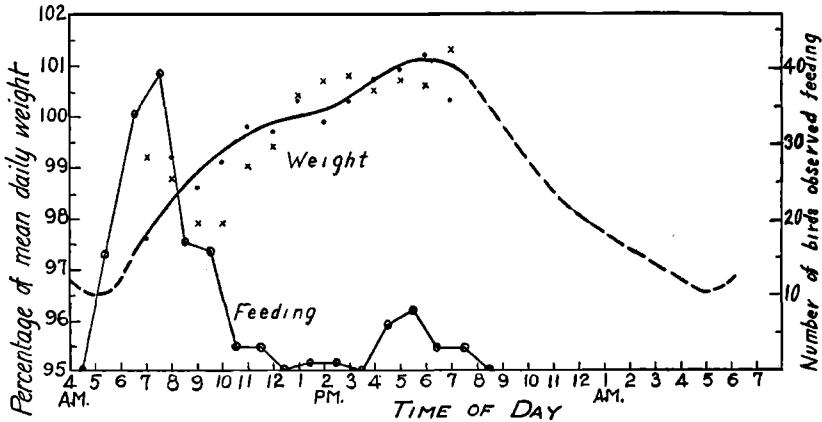


TEXT-FIG. 2.—Hourly fluctuations in weight of individual birds on single days while living freely in the natural wild state. A—Chipping Sparrow, F-45368, immature, July 31, 1931; B—Chipping Sparrow, F-45368, immature, July 25, 1931; C—Chipping Sparrow, C-68760, female, June 24, 1930; D—Song Sparrow, B-165841, female (?), July 11, 1932; E—Song Sparrow, B-189226, female (?), April 27, 1932; F—Song Sparrow, B-189217, male (?), April 27, 1932; G—Cowbird, A-288170, immature, July 14, 1933; H—Cowbird, A-288173, immature, July 22, 1933; I—the same, July 15, 1933.

into this composite curve are Chipping Sparrow, Song Sparrow, Field Sparrow, English Sparrow, Catbird, Cowbird, House Wren, and Mourning Dove. The curve is extended on a hypothetical basis to include the rest of the day as well.

At night the curve is drawn to show the drop in weight somewhat more rapid early in the evening than later. This is surmised from the fact that the birds are more restless then than they are later during the night, and there is elimination of undigested food material from the alimentary tract.

After an hour or so when the birds have settled down, the metabolic rate and body temperature may become reduced to the standard level as the birds attain a post-absorptive condition, and the weight loss is probably uniform. Birds are even more quiet after midnight than before, which implies a slower rate of weight loss, but this is offset by lower air temperatures which then prevail and which may induce an increase in the loss of weight.



TEXT-FIG. 3.—Average daily rhythm in body weight of several species of birds during summer months. Dots represent data for adults; crosses represent data for immatures; the heavy full line is the smoothed curve drawn through these data for adults; the broken line is interpolated to indicate approximately how the birds' weight varies during the other hours of the day when no weights were obtained. The thin line represents number of birds observed per hour feeding in a natural habitat (Long).

During most of the morning there is a gradual weight increase due, apparently, to active feeding. From about 11.00 a.m. to 3.00 p.m. the increase in body weight becomes small, probably due to the less active feeding. In late afternoon there is again an acceleration of weight increase which may be correlated again with the more active feeding. The general similarity between this curve and many of the curves shown in Text-figs. 1 and 2 is apparent, although here many of the fluctuations characteristic of individual birds for individual days are eliminated.

The curve in Text-fig. 3 showing the amount of feeding throughout the day was kindly furnished by Mr. William H. Long, and is the result of intensive study of bird activities under natural conditions out-of-doors, made when he was engaged in the Williamston Wildlife Management Project, School of Forestry and Conservation, University of Michigan. The curve summarizes records of 422 individuals of forty-one mostly passerine species during July, 1931, on an area of ungrazed farmland. The correlation between the curves in this figure is most significant since they were made by

different workers in different localities independently of one another and combined in the same chart without further modification. Flentge (1937) has also attempted recently to learn the principal times of day for feeding from the number of birds captured in banding traps. When his data are put on an hourly basis, they agree well with the curve in Text-fig. 3 except that he found a relatively larger number of birds coming to the traps between 5.00 p.m. and darkness than at any other time of the day. In Text-fig. 3, data for immature birds are also inserted. These data were prepared as for the adults; they are averages for all species for the three summer months. It will be noted that all points fall around the curve for adult birds, although there are some differences which may prove to be significant.

The time at which the maximum weight is attained may fall on almost any hour in the afternoon although in the composite curve it comes at 6.00 o'clock in the adults and at 7.00 o'clock in the immatures. This was well shown in a separate study of the average daily rhythm of each species during all months where data were available and also of similar data for Tree Sparrow, Slate-colored Junco, White-crowned Sparrow, and White-throated Sparrow. The maximum weight came most frequently (five times) at 7 p.m., four times each at 8 p.m. and 4 p.m., and nine times at five other hours. Late afternoon and evening, therefore, seem to be the most typical time for birds to attain their maximum weight. The minimum weight is probably attained soon after the birds begin activities in the very early morning and before they have begun to fill their stomachs with food. In the summer, this would be at some time around 5 a.m. Such actual minimum weights were probably not obtained in this study, although random fluctuations to very low weights occurred irregularly at various hours later in the morning.

The difference between the extreme values for adults shown in Text-fig. 3 is approximately 4.5 per cent, if the interpolated value for 5.00 o'clock a.m. is used, or 3.5 per cent if the value at 7.00 o'clock is considered the minimum. This agrees well with weight variations of birds in the wild found by other workers but, nevertheless, does not represent the extent of variation in the weight of individual birds for single days. Using a table of data, not incorporated in this paper, giving the average daily rhythm in weight of each of the above species for many months of the year, a preliminary study of the supposed maximum daily weight variation showed an interesting statistical phenomenon. Nine sets of data each with an average of less than ten weights per hour had an average extreme weight variation during the day of 13.4 per cent; six sets of data each with from ten to seventeen weights per hour had an average variation of 11.6 per cent; four sets of data with from twenty to twenty-six weights per hour had 7.2 per cent maximum variation; while two sets of data with sixty-four and eighty weights per hour showed

only 4.1 and 4.9 per cent variations, respectively. The more numerous the data, the less the maximum percentage variation became. One reason for this is that the hour at which the minimum and maximum weights, especially the maximum weights, were attained varied so greatly on different days and with different individuals that when all weights for each hour for many individuals were averaged, true maximum and minimum values were lost. This was further shown from a study of weight variations during the day of individual birds that came to the traps and were weighed at least once in the morning and once in the afternoon. In a total of 655 days' records for eighteen passerine species, the greatest weight came in the afternoon on 65 per cent of the days, while on the other 35 per cent of the days, the greatest weight came some time in the morning. The random manner in which the weight of birds in Nature may fluctuate is shown in Text-fig. 2, yet if the birds' weight were continuously recorded, one would probably find a greater percentage of the maximum weights coming in the afternoon. Thus, the average of scattered weights of many individuals over many days tends to eliminate extreme values and does not show the true extent to which an individual bird may vary.

An attempt was then made to determine the extreme variation in weights of individual birds only for the more typical cases where their maximum weights came in the afternoon. With 252 different individual birds belonging to seventeen species and covering 429 days, this variation in percentage of their mean weight amounted to 5.4 ± 0.36 per cent. Even this is not as great as it should be because in most cases only two or three weights of a bird were available for single days and so the truly extreme weights for the day were probably measured in only a very small percentage of the cases. Nevertheless, this 5.4 per cent of variation approaches the 5.9 per cent variation between the extreme weights of the birds shown in Text-fig. 1, *if* the first early-morning weight before feeding commences is omitted. Probably in very few instances, if any, were truly minimum weights, such as occur early in the morning, measured with birds caught in the traps. It seems not unlikely that, if these could be obtained, extreme variations of from 8 to 12 per cent as noted by ourselves and by Taber (1928), Nice (1929), Sumner (1935), and Stewart (1937) in experimental birds would not be out of harmony with what frequently occurs in wild birds living freely in Nature. One may expect, however, that the extent of the daily fluctuation in weight may vary under different environmental circumstances, especially, as will be later shown, with air temperature.

MONTHLY VARIATIONS IN WEIGHT

More literature is available on monthly variations during the year in weight of birds than on hourly variations during the day. Wilson (1911,

vide Stresemann, 1927) gives a yearly curve for a grouse, *Lagopus scoticus*, which is somewhat irregular. The male showed highest weights from December to February and again in August, with lowest weights occurring in March and again in September and October. The female generally increased in weight from November to April and decreased from April to November. Stieve (1922) found that captive geese decreased about 25 per cent as the gonads matured during the breeding season. Zedlitz (1926) made an intensive study of monthly variations in the weight of several species of European birds. With few exceptions, all species weighed most in winter and early spring, decreased during the breeding season, and then increased during the following autumn. Weigold (1926) adds confirmatory records.

Song Sparrows that winter in an area or migrate through it early in the spring have been noted by several observers to be heavier than those that breed in the same region in the summer (Whittle, 1927, 1929; Myers, 1928; Hoffman, 1930; Wetherbee, 1934; Nice, 1934). Nice (1937) shows that Song Sparrows are somewhat low in autumn, reach their maximum in late December, January, and early February, gradually decrease to April and from then on (except for laying females) decrease to a lower point than in autumn. Males in January weighed 11 per cent higher than in April, females 7.5 per cent higher. Recently (1938) she has shown winter increases in weight for other species. Stewart (1937) obtained 215 weights of Song Sparrows between August and April. The birds' weight increased regularly from August to a maximum in January, then decreased to April. With the Scaled Quail (*Callipepla squamata*) in New Mexico, Russell (1931) reports maximum weights in February and minimum weights in August. No data are available for the months, November to January. In captive male *Fringilla coelebs*, Groebbels (1932) found minimum weights to occur in January and an increase to a maximum in March, April and May. Contrary results were obtained with captive male *Phoenicurus phoenicurus* and *Turdus merula*, for with these species, greatest weights came in the winter, while during March, April, and May, there was a decided drop in weight with the onset of singing. During the summer months weights again increased. Weight variations in captive birds may often require special explanation and may often not represent conditions in the wild. With *Sylvia communis* not in captivity, he found a decrease in weight from middle March to middle May, a maintenance of low weight during the summer, and an increase again in the autumn. Hicks (1934) found that the weight of male and female Starlings increased during the winter from December to early February, when the maximum was reached, then decreased through March. Kendeigh (1934) showed that winter weights of English Sparrows were greater than summer weights.

Linsdale and Sumner (1934b) found in a large number of weighings of the Golden-crowned Sparrow and the Fox Sparrow an increase in weight from October until a peak was reached in mid-winter (about January) and that another even higher peak was reached in May just before the spring migration. Supplementary information indicated that this weight was maintained until arrival on the breeding grounds. Some evidence indicated a decrease in weight during midsummer. In a later study of Spotted Towhees, Linsdale and Sumner (1937) found somewhat similar monthly variations in weight on the basis of more fragmentary data, although they state that male towhees did not show a peak in weight just before migration in the spring as did the two other species with which they worked.

Heydweiller (1935a, b) studied weights of Tree Sparrows on their wintering grounds around Ithaca, New York, and on their breeding grounds around Churchill, Manitoba. Maximum weights of males (21.2 grams) and females (20.2 grams) were attained during the first week of March. In late March and April a decrease of 10 per cent in their weights occurred. On the breeding grounds in July and early August, both males and females decreased still further in weight to a minimum of 82 per cent of their maximum spring weight. During the third week of August the adults began to increase in weight. Only nine weights were taken in August and the number available for other months is not given.

Shaw (1935) in China, analyzed 287 weights of the Tree Sparrow, *Passer montanus saturatus*, and came to the conclusion that seasonal variation of body weight was very slight. However, a study of his table of average monthly weights of males and females discloses that the weights of the species during March, April, and May are predominantly above the average and during June, July, and August below the average.

In Sumner's (1935) study of the California Quail, weight curves are given showing monthly variations separately in male and female. The males weighed the most from December to March and the least from late April to July. The female's weight was high from December on through the winter but did not reach its maximum until May, while it was lowest from July to November, thus lagging behind the male in its variations.

Stoner (1936) gives information on the weight of the Bank Swallow (*Riparia r. riparia*), indicating a progressive decrease from May to June to July.

That the size or weight of birds varies during different portions of the spring and autumn migration periods is known. Allen (1871) stated long ago: "In the Anatidae and *Tringa*, which breed far to the northward and pass the winter in lower latitudes, it is noticeable that, those which arrive first in the fall, and those which return north latest in the spring, are smaller than those that arrive later and depart earlier, . . . This has been

especially noticed in species of *Fulix*, *Bernicla*, *Actodromas*, and *Macrorhamphus*." Recent studies of Kendeigh (1934) show similar relations between times of migration and weights of White-crowned and White-throated Sparrows. Wetherbee (1934) also found that Myrtle Warblers (*Dendroica coronata*) migrating late in the autumn are heavier than those individuals migrating earlier. In general, the evidence from the literature indicates that, with some exceptions, birds tend to weigh most during the winter or spring and least during the summer or early autumn. The exact time at which the minimum and maximum weights are attained may vary with the sex and the species, and presumably may also be influenced by differences in environmental conditions due to locality and by breeding factors. A great variety of reasons is given in explanation of these hourly and monthly changes in bird weight although there is very little detailed analysis or experimental verification. The increase in weight during the daytime and the decrease at night are generally explained by the consumption of food (and water) during the daytime and its utilization without replacement at night. The extent of the daily fluctuation in weight would be correlated, apparently, with the capacity of the digestive tract to hold food.

Monthly changes in the weights of a species are sometimes believed to be due to variations in the individuals or to the proportion of immatures and adults composing the bird population (Hicks, 1934). Such variations in the population of a species at different times of the year do occur (Starling), especially during migration, and may in some cases explain the changes noted in the weight of the species. In at least some instances (Song Sparrow) these weight differences have been correlated with size differences in the different individuals involved (Wetherbee, 1934). Numerous records obtained by Linsdale and Sumner (1934b), Nice (1937), and Stewart (1937) of weights of the same individual banded birds at various times of the year show variations similar to those of the species as a whole; these monthly variations in weight are, therefore, not everywhere to be explained merely by the shifting constitution of the population of the species. Likewise, the increasing weights obtained for the species during the autumn and winter cannot be due simply to the increasing age of the younger birds, for they hold true for adults, taken separately, as well. In some passerine species immature birds closely approximate the adults in weight within two or three months or by early autumn (Linsdale, 1928; Partin, 1933; Shaw, 1935; Nice, 1937). The decrease in weight during the spring or summer is obviously not due simply to increasing age of the immatures in the population even if the increase in weight during the autumn could be thus explained.

Variation in the abundance of food, or, at least, variation in the amount of feeding, is mentioned incidentally by many authors as the cause of weight fluctuations. The drop in weight during the late spring and summer is

ascribed to the irregular feeding of the birds at that time because of the greater activity involved in singing, in caring for the young, and of the long periods of sitting on the eggs during incubation. During other seasons, a part or all of this time may be devoted to feeding. Some correlation has also been attempted with length of day and amount of activity. Some think a drop in weight may be caused by a high nervous excitement involved in mating and nesting, as well as by the actual energy requirements for spermatogenesis and oogenesis, for increase in size of the gonads, for molting and renewal of feathers, and for the act of migration. The energy requirements and the energy production of birds at different seasons of the year have never been satisfactorily measured in full. In Kendeigh and Baldwin's (1937) analysis of the factors affecting the abundance and distribution of the House Wren, it was shown that breeding does require a certain amount of energy over and above that necessary merely for existence, but this was compensated for, in part at least, by the distribution during the breeding season being limited to more moderate climatic regions than during other periods of the year. The possibility distinctly exists that excess needs at one season, as for nesting or molting, are balanced by other needs at other seasons, as for migration, or, in winter, for increased resistance to lower temperatures and longer nights. The suggestion that birds, by becoming fat at certain seasons, unconsciously foresee migration or breeding or wintering conditions of any other energy requirement seems unjustified. More probably the functions of birds respond to forces acting at the moment or in the past.

Fluctuations in bird weights may be correlated with amount of feeding or with rates of energy utilization or with both together. There still remains the question as to which are causes and which are effects, or whether variations in weight, feeding, and energy utilization are dependent upon some other factor not yet mentioned. Some suggest as a factor the existence in the bird of internal physiological rhythms involving glandular changes, ratio between anabolism and katabolism, or other conditions. Bird students in California have found, for instance, that the females of certain species (Fox Sparrow, Shrike, House Finch, California Quail) are heavier in relation to the male during the early breeding period than they are at other times (Linsdale, 1928; Miller, 1931; Partin, 1933; Sumner, 1935). This has been shown also for the Scaled Quail (Russell, 1931) and Song Sparrow (Nice, 1937). In experimental work with captive male geese on the other hand, Stieve (1922) found that the gonads did not develop normally without a corresponding decrease in body weight. Seasonal changes in weight may possibly be correlated also with changes in size and rate of functioning of such internal organs as liver, spleen, and thyroid (Riddle, 1928), or with length of digestive tract or other organs.

Monthly averages of body weight were obtained in this study for several species of birds available from the banding traps. These are presented in Table 5. Averages are presented for each sex separately, for adults regardless of sex, occasionally an average of the weights of the two adult sexes, for immatures, occasionally for all individuals of a species regardless of sex and age, and separately for those whose age and sex were unknown. Usually adults and immatures are not separated after October but all individuals classed as adults. The total number of records for adult birds is frequently more than the combined records given separately for the sexes because many adults were not sexed when weighed. Since records were obtained with fair uniformity in both forenoon and afternoon during all seasons, the daily-rhythm factor is largely eliminated.

In the analysis of the records, major emphasis is placed on average weight of all the adults, since both sexes are included in the data for each month. Discrepancies between the sexes in monthly weight variations are worthy of note. For instance, there is some evidence that females differ from males by increasing in weight during the egg-laying period, as was noted in the literature above. As shown in Table 5, female Song Sparrows in May dropped in weight from what they were in April, although this drop was less than the drop in the males, and the females more nearly approached the males in weight during this month than at any other time. In June, the females dropped in weight considerably more than did the males. The female Chipping Sparrows appeared to increase in weight from April to June while the males were decreasing, yet the number of weights obtained during April is not sufficient to be entirely trustworthy. There seems also to be an increase in weight of female Cowbirds, Towhees, and Downy Woodpeckers during May which lends suspicion to the truth of this hypothesis. Yet considerably more data are required before the possibility can be eliminated that the variations may be due to random sampling or to other causes. Variation in the monthly average weight of males also occurs, which, if substantiated by more information, likewise needs to be explained. Differences between sexes in monthly variations are of less concern in the present investigation than are the broad general trends throughout the year that seem best represented by combining the weights for both sexes.

Considering all the data for adult birds in Table 5, an analysis shows that the lowest weight comes in July for nine species, in August for five species, in June for four species and in other scattered months for another four species. Only in the White-breasted Nuthatch are the lowest weights found in winter. This species is peculiar in that its weight falls almost as low in July as in winter and averages higher in both spring and autumn. An average of all species clearly shows the minimum weight in July.

In general, the weights increase month by month until mid-winter, then

TABLE 5
Monthly Record of the Weights of Wild Birds, listed in the Order of Abundance of Data

Species	Age and Sex	January		February		March		April		May		June	
		Number Records	Average Weight	Number Records	Average Weight	Number Records	Average Weight	Number Records	Average Weight	Number Records	Average Weight	Number Records	Average Weight
Song Sparrow, <i>Melospiza melodia</i>	M.	—	—	—	—	—	—	176	21.5	112	20.8	96	20.7
	F.	—	—	—	—	—	45	21.0	45	20.6	72	19.7	
	Immn.	1	22.9	3	24.1	26	22.4	464	21.4	382	21.1	293	19.9
Chipping Sparrow, <i>Spizella passerina</i>	M.	—	—	—	—	—	—	34	12.7	406	12.2	133	12.1
	F.	—	—	—	—	—	—	14	11.9	248	12.2	128	12.2
	Immn.	—	—	—	—	—	—	237	12.6	1203	12.3	397	12.2
White-throated Sparrow, <i>Zonotrichia albicollis</i>	Ads.	—	—	—	—	—	—	16	28.7	90	29.4	—	—
	Immn.	—	—	—	—	—	—	—	—	—	—	—	—
	All	—	—	—	—	—	—	—	—	—	—	—	—
Field Sparrow, <i>Spizella pusilla</i>	M.	—	—	—	—	—	—	24	12.8	44	12.5	—	—
	F.	—	—	—	—	—	—	2	11.6	6	12.8	3	13.4
	Immn.	—	—	—	—	—	—	157	12.9	205	12.8	4	12.8
Slate-colored Junco, <i>Junco hyemalis</i>	M.	—	—	—	—	—	—	54	21.4	—	—	—	—
	F.	—	—	—	—	—	—	63	19.9	—	—	—	—
	All	1	19.6	8	22.6	19	21.0	366	21.0	—	—	—	—
English Sparrow, <i>Passer domesticus</i>	M.	34	29.9	19	28.6	6	29.7	1	26.5	1	27.0	4	27.2
	F.	33	28.2	20	28.3	6	29.0	2	30.0	—	—	3	28.1
	Immn.	72	29.1	40	28.5	18	29.5	6	29.3	1	27.0	7	27.6
Tree Sparrow, <i>Spizella arborea</i>	All	8	20.1	29	21.6	79	19.6	346	19.3	—	—	—	—
Catbird, <i>Dumetella carolinensis</i>	M.	—	—	—	—	—	—	—	—	24	35.3	25	34.2
	F.	—	—	—	—	—	—	—	—	43	38.4	39	36.3
	Immn.	—	—	—	—	—	—	—	—	139	36.4	116	35.4
Cowbird, <i>Molothrus ater</i>	M.	—	—	—	—	—	—	14	45.5	10	47.4	5	47.7
	F.	—	—	—	—	—	—	15	37.5	19	38.6	28	39.8
	Immn.	—	—	—	—	—	—	—	41.5	—	43.0	36	43.8

The American Ornithologists' Union 'Check-list,' fourth edition, 1931, is followed for the scientific names of the species. Subspecies are not considered in this report, since no attention was given to their identification and since the subspecific status of some local birds is uncertain. All weights were obtained from birds in the vicinity of Cleveland, Ohio.

TABLE 5—(Continued)
Monthly Record of the Weights of Wild Birds, listed in the Order of Abundance of Data

Species	Age and Sex	July		August		September		October		November		December	
		Number Records	Average Weight	Number Records	Average Weight	Number Records	Average Weight	Number Records	Average Weight	Number Records	Average Weight	Number Records	Average Weight
Song Sparrow, <i>Melospiza melodia</i>	M.	75	20.7	18	21.1	9	23.2	3	22.9	—	—	—	—
	F.	43	20.2	37	20.1	5	21.6	—	—	—	—	—	—
	Ads. Imm.	331 962	19.8 19.1	83 741	20.6 20.0	24 354	22.7 21.1	13 56	21.7 21.7	3	20.9	1	26.0
Chipping Sparrow, <i>Spizella passerina</i>	M.	51	12.0	36	12.0	7	12.9	—	—	—	—	—	—
	F.	73	12.0	12	11.6	16	12.1	—	—	—	—	—	—
	Ads. Imm.	217 90	11.8 11.4	85 215	12.0 11.8	70 132	12.4 12.3	8 10	13.4 13.4	—	—	—	—
White-throated Sparrow, <i>Zonotrichia albicollis</i>	Ads. Imm.	—	—	—	—	—	—	151	26.3	—	—	—	—
	All	—	—	—	—	118	25.1	233	25.5	12	28.2	—	—
Field Sparrow, <i>Spizella pusilla</i>	M.	—	—	11	12.9	8	12.9	—	—	—	—	—	—
	F.	4	10.9	3	13.7	—	—	—	—	—	—	—	—
	Ads. Imm.	8 15	11.2 12.2	42 113	12.7 12.4	130 109	13.0 12.9	67 15	13.0 13.0	—	1	19.0	—
Slate-colored Junco, <i>Junco hyemalis</i>	M.	—	—	—	—	—	—	—	—	—	—	—	—
	F.	—	—	—	—	—	—	—	—	—	—	—	—
	Ads. Imm. All	—	—	—	—	—	—	—	—	—	—	—	—
English Sparrow, <i>Passer domesticus</i>	M.	7	26.5	4	26.1	3	27.1	3	27.1	—	—	—	—
	F.	6	26.2	2	32.3	1	26.7	3	25.4	—	—	—	—
	Ads. Imm. All	13 156	27.3 25.7	6 208	28.2 27.0	4 33	27.0 27.6	6 20	26.3 27.8	—	—	—	—
Tree Sparrow, <i>Spizella arborea</i>	M.	—	—	—	—	—	—	—	—	—	—	—	—
	All	—	—	—	—	—	—	—	—	4	19.1	6	21.1
Catbird, <i>Dumetella carolinensis</i>	M.	21	32.7	—	—	3	40.7	—	—	—	—	—	—
	F.	20	34.7	1	35.9	1	37.1	—	—	—	—	—	—
	Ads. Imm.	49 75	33.9 34.9	8 38	35.9 34.7	7 6	40.5 35.5	—	—	—	—	—	—
Cowbird, <i>Molothrus ater</i>	M.	5	45.0	—	—	—	—	—	—	—	—	—	—
	F.	11	39.0	2	41.0	2	35.3	—	—	—	—	—	—
	Avg. Imm.	— 212	42.0 36.8	— 33	— 36.7	— 1	— 45.2	—	—	—	—	—	—

TABLE 5—(Continued)
 Monthly Record of the Weights of Wild Birds, listed in the Order of Abundance of Data

Species	Age and Sex	January		February		March		April		May		June	
		Number Records	Average Weight	Number Records	Average Weight	Number Records	Average Weight	Number Records	Average Weight	Number Records	Average Weight	Number Records	Average Weight
White-crowned Sparrow, <i>Zonotrichia leucophrys</i>	Ads. Immn.	—	—	—	—	—	—	—	—	151	32.8	—	—
	M.	—	—	—	—	—	—	1	10.9	31	11.1	31	10.5
	F.	—	—	—	—	—	—	1	13.0	9	11.3	31	11.7
House Wren, <i>Troglodytes aëdon</i>	Ads. Immn.	—	—	—	—	—	—	2	12.0	40	11.1	63	11.1
	M.	—	—	—	—	—	—	11	43.5	10	41.7	1	43.1
	F.	—	—	—	—	3	42.4	3	41.5	13	44.1	—	—
Towhee, <i>Pipilo erythrophthalmus</i>	Ads. Immn.	—	—	—	—	6	42.4	15	43.0	25	42.7	1	43.1
	M.	—	—	—	—	—	—	—	—	—	—	—	—
	F.	—	—	—	—	—	—	—	—	—	—	—	—
Mourning Dove, <i>Zenaidura macroura</i>	Ads. Immn.	—	—	—	—	—	—	5	136.8	9	147.4	15	137.7
	M.	—	—	—	—	—	—	10	132.9	9	139.0	4	144.4
	F.	—	—	—	—	—	—	—	—	30	144.6	45	138.5
Downy Woodpecker, <i>Dryobates pubescens</i>	Ads. Immn.	3	27.9	3	26.9	5	27.4	6	28.2	19	28.3	11	27.9
	M.	1	30.4	1	27.6	6	27.6	10	27.4	13	28.1	8	25.4
	F.	4	28.6	4	27.1	11	27.7	16	27.7	32	28.2	19	26.8
Black-capped Chickadee, <i>Penthestes atricapillus</i>	Ads. Immn.	—	—	—	—	—	—	3	10.8	1	11.6	3	10.0
	M.	—	—	—	—	—	—	8	10.0	3	10.7	3	9.9
	F.	20	12.0	16	10.9	11	11.1	31	11.1	16	11.2	10	10.4
Cardinal, <i>Richmondia cardinalis</i>	Ads. Immn.	—	—	—	—	—	—	—	—	—	—	—	—
	M.	1	49.7	2	44.2	14	45.4	5	44.4	7	41.7	4	41.1
	F.	1	50.3	7	44.7	7	44.7	1	44.3	1	44.7	1	39.5
Brown Thrasher, <i>Toxostoma rufum</i>	Ads. Immn.	—	—	—	—	21	45.2	7	44.0	8	42.1	5	40.8
	M.	—	—	—	—	—	—	—	—	—	—	1	42.8
	F.	—	—	—	—	—	—	4	69.4	6	73.0	5	64.8
White-breasted Nuthatch, <i>Sitta carolinensis</i>	Ads. Immn.	—	—	—	—	—	—	—	—	—	—	27	61.9
	M.	2	21.1	3	21.3	1	21.0	3	20.9	4	22.3	1	21.7
	F.	7	20.8	5	20.8	5	21.3	10	21.6	4	21.6	1	20.7
?	—	—	—	—	—	—	—	—	—	8	22.0	4	21.3
?	—	—	—	—	—	—	—	—	—	—	—	2	19.4

TABLE 5—(Continued)
 Monthly Record of the Weights of Wild Birds, listed in the Order of Abundance of Data

Species	Age and Sex	January		February		March		April		May		June	
		Number	Average Weight	Number	Average Weight	Number	Average Weight	Number	Average Weight	Number	Average Weight	Number	Average Weight
Tufted Titmouse, <i>Parus bicolor</i>	M.	—	—	—	—	—	—	7	20.7	—	—	6	21.4
	F. Ads.	6	22.4	4	23.6	2	22.0	7	20.7	5	22.4	7	21.2
	Imm.	—	—	—	—	—	—	—	—	—	—	2	19.6
Robin, <i>Turdus migratorius</i>	M.	—	—	—	—	—	—	2	73.9	3	79.6	3	81.4
	F. Ads.	—	—	—	—	—	—	1	52.8	1	77.2	4	78.6
	Imm.	—	—	—	—	5	77.4	3	76.9	4	79.0	10	70.5
Blue Jay, <i>Cyanocitta cristata</i>	M.	—	—	—	—	—	—	1	83.8	7	86.1	1	87.1
	F. Ads.	1	95.0	—	—	—	—	4	80.8	8	85.5	33	76.3
	Imm.	—	—	—	—	—	—	—	—	—	—	42	77.5
Bobwhite, <i>Colinus virginianus</i>	M.	—	—	—	—	—	—	—	—	—	—	—	—
	F. Ads.	—	—	—	—	—	—	3	196.8	1	171.4	1	184.3
	Imm.	—	—	—	—	—	—	4	189.8	2	196.2	1	184.3
Starling, <i>Sturnus vulgaris</i>	M.	—	—	—	—	—	—	—	—	—	—	—	—
	F. Ads.	—	—	2	80.8	2	85.6	—	—	—	—	1	81.3
	Imm.	—	—	7	85.9	6	86.2	—	—	—	—	2	78.6
Vesper Sparrow, <i>Pooecetes gramineus</i>	M.	—	—	—	—	—	—	—	—	—	—	—	—
	F. Ads.	—	—	—	—	—	—	—	—	—	—	—	—
	Imm.	—	—	—	—	—	—	2	27.6	3	25.2	1	24.6
Bluebird, <i>Sialia sialis</i>	M.	—	—	—	—	—	—	—	—	—	—	—	—
	F. Ads.	—	—	—	—	—	—	—	—	—	—	—	—
	Imm.	—	—	—	—	—	—	10	33.8	3	33.7	2	30.2
Hairy Woodpecker, <i>Dryobates villosus</i>	M.	—	—	—	—	—	—	—	—	—	—	—	—
	F. Ads.	—	—	1	61.6	—	—	3	68.0	5	70.3	2	68.6
	Imm.	—	—	—	—	1	62.4	1	63.1	2	59.2	2	57.8
Goldfinch, <i>Spinus tristis</i>	M.	—	—	—	—	—	—	—	—	—	—	—	—
	F. Ads.	—	—	—	—	—	—	—	—	—	—	—	—
	Imm.	—	—	—	—	—	—	—	—	—	—	—	—
Fox Sparrow, <i>Passerella iliaca</i>	M.	—	—	—	—	—	—	—	—	—	—	—	—
	All	—	—	—	—	—	—	9	36.6	—	—	—	—

TABLE 5—(Continued)
Miscellaneous Records (in A. O. U. Check-list Order)

Species	Month	Age and sex	Number of records	Average weight
Least Bittern, <i>Ixobrychus exilis</i>	May	M.	1	64.8
Broad-winged Hawk, <i>Buteo platypterus</i>	May	M.	2	363.8
Sparrow Hawk, <i>Falco sparverius</i>	July	F.	1	113.5
Golden Plover, <i>Pluvialis dominica</i>	November	Imm.	1	136.2
Spotted Sandpiper, <i>Actitis macularia</i>	May	F.	1	40.4
Yellow-billed Cuckoo, <i>Coccyzus americanus</i>	August	M.	1	57.8
Screech Owl, <i>Otus asio</i>	September	Imm.	1	175.7
Ruby-throated Hummingbird, <i>Archilochus colubris</i>	May	M.	1	3.0
	July	M.	1	2.5
	August	?	1	3.2
	September	?	1	3.2
Belted Kingfisher, <i>Megaceryle alcyon</i>	September	?	2	133.4
Flicker, <i>Colaptes auratus</i>	May	M.	1	123.6
	June	M.	2	137.6
		F.	2	131.0
		Imm.	1	75.2
	July	Imm.	1	108.8
	August	?	1	109.7
	September	?	1	148.9
	October	?	1	130.1
Red-headed Woodpecker, <i>Melanerpes erythrocephalus</i>	May	M.	1	73.2
Crested Flycatcher, <i>Myiarchus crinitus</i>	July	F.	1	30.9
	August	?	1	28.7
Eastern Phoebe, <i>Sayornis phoebe</i>	May	F.	1	18.9
	June	M.	1	20.0
		F.	1	19.2
	August	F.	2	16.1
		Imm.	2	13.4
		?	6	17.5
	September	?	3	19.0
Yellow-bellied Flycatcher, <i>Empidonax flaviventris</i>	September	F.	1	11.8
Wood Pewee, <i>Myiochanes virens</i>	August	Imm.	1	13.0
		?	2	12.8
Purple Martin, <i>Progne subis</i>	July	F.	1	46.4
Crow, <i>Corvus brachyrhynchos</i>	June	M.	1	479.0
		Imm.	3	457.4
	July	Imm.	2	454.3
Red-breasted Nuthatch, <i>Sitta canadensis</i>	February	M.	1	11.8
Brown Creeper, <i>Certhia familiaris</i>	October	Imm.	2	8.8
Winter Wren, <i>Tannus hiemalis</i>	April	F.	1	9.7
	October	F.	2	9.3
	November	Imm.	1	9.6

TABLE 5—(Continued)
Miscellaneous Records (in A. O. U. Check-list Order)

Species	Month	Age and sex	Number of records	Average weight	
Wood Thrush, <i>Hylocichla mustelina</i>	May	F.	2	48.8	
	August	F.	1	53.8	
Hermit Thrush, <i>Hylocichla guttata</i>	April	M.	1	32.7	
	May	Ads.	1	28.1	
	October	F.	1	31.4	
		Imm.	1	30.2	
Olive-backed Thrush, <i>Hylocichla ustulata</i>	September	M.	3	30.6	
		Imm.	2	34.1	
Gray-cheeked Thrush, <i>Hylocichla minima</i>	October	Imm.	1	43.7	
	September	Imm.	1	31.7	
		?	1	30.6	
Golden-crowned Kinglet, <i>Regulus satrapa</i>	October	Imm.	2	6.2	
Ruby-crowned Kinglet, <i>Corthylio calendula</i>	October	Imm.	1	6.0	
Cedar Waxwing, <i>Bombycilla cedrorum</i>	August	Imm.	1	25.9	
Northern Shrike, <i>Lanius borealis</i>	January	Imm.	1	56.8	
Blue-headed Vireo, <i>Vireo solitarius</i>	September	Imm.	1	19.3	
	Red-eyed Vireo, <i>Vireo olivaceus</i>	May	M.	1	16.5
			F.	1	15.6
		June	M.	1	16.3
		July	M.	1	17.5
		August	M.	1	15.5
			F.	1	15.5
			?	4	16.5
		September	F.	1	19.5
			Imm.	1	17.4
		?	4	18.8	
Warbling Vireo, <i>Vireo gilvus</i>	August	?	1	11.7	
Black and White Warbler, <i>Mniotilta varia</i>	May	M.	1	10.8	
	August	M.	2	11.2	
		F.	1	9.2	
Tennessee Warbler, <i>Vermivora peregrina</i>	September	Imm.	1	9.5	
	October	Imm.	1	8.8	
Nashville Warbler, <i>Vermivora ruficapilla</i>	September	Imm.	1	9.5	
Yellow Warbler, <i>Dendroica aestiva</i>	May	Ads.	2	9.6	
	July	Imm.	1	9.7	
	August	Imm.	2	11.0	
Cape May Warbler, <i>Dendroica tigrina</i>	August	Imm.	1	10.0	
	September	Imm.	2	10.4	
Myrtle Warbler, <i>Dendroica coronata</i>	April	F.	1	16.8 ¹	
	May	F.	3	13.8	
	October	Imm.	1	12.4	
		?	1	14.0	

¹ Very fat.

TABLE 5—(Continued)
Miscellaneous Records (in A. O. U. Check-list Order)

Species	Month	Age and sex	Number of records	Average weight
Black-throated Green Warbler, <i>Dendroica virens</i>	July	M.	1	9.6
	September	M.	1	9.6
		Imm.	5	8.8
	October	Imm.	1	10.1
Blackburnian Warbler, <i>Dendroica fusca</i>	May	M.	1	11.1
	September	F.	1	9.5
Chestnut-sided Warbler, <i>Dendroica pensylvanica</i> .	August	Imm.	1	8.9
Bay-breasted Warbler, <i>Dendroica castanea</i>	September	F.	1	10.8
		Imm.	1	10.0
		Ads.	1	12.4
Black-poll Warbler, <i>Dendroica striata</i>	May	Ads.	1	12.4
	September	M.	3	11.4
		F.	1	12.8
		Imm.	3	11.5
	October	Imm.	4	13.9
	Oven-bird, <i>Seiurus aurocapillus</i>	May	M.	2
F.			1	19.1
August		F.	2	20.2
		Imm.	2	20.0
		?	2	16.0
Water-Thrush, <i>Seiurus noveboracensis</i>	September	?	1	20.0
Mourning Warbler, <i>Oporornis philadelphia</i>	September	M.	1	11.2
Yellow-throat, <i>Geothlypis trichas</i>	August	M.	1	11.1
	September	M.	1	9.9
		F.	1	7.2
Redstart, <i>Setophaga ruticilla</i>	May	M.	2	7.8
	August	M.	1	8.2
		F.	1	7.2
	September	M.	1	8.8
		Imm.	2	8.5
Red-winged Blackbird, <i>Agelaius phoeniceus</i>	July	M.	1	61.4
Baltimore Oriole, <i>Icterus galbula</i>	May	F.	1	34.2
	July	Imm.	3	33.3
	August	Imm.	1	32.5
		?	2	32.7
Bronzed Grackle, <i>Quiscalus quiscula</i>	April	M.	2	129.0
		F.	2	98.9
	June	M.	1	102.9
	July	M.	1	110.0
	May	M.	1	24.0
Scarlet Tanager, <i>Piranga erythromelas</i>	May	M.	1	24.0
Rose-breasted Grosbeak, <i>Hedymeles ludovicianus</i> .	August	Imm.	2	40.2
Indigo Bunting, <i>Passerina cyanea</i>	June	M.	1	15.6
	August	F.	1	12.9
	September	Imm.	2	14.2

TABLE 5—(Continued)
Miscellaneous Records (in A. O. U. Check-list Order)

Species	Month	Age and sex	Number of records	Average weight
Purple Finch, <i>Carpodacus purpureus</i>	January	M.	1	25.9
		Imm.	1	24.6
	February	M.	4	25.4
	March	F.	1	25.4
	July	Imm.	3	23.2
Savannah Sparrow, <i>Passerculus sandwichensis</i>	October	Imm.	1	41.6
	July	M.	2	18.8
	August	M.	1	18.8
	September	M.	1	16.7
Lincoln's Sparrow, <i>Melospiza lincolni</i>	?	?	1	17.8
	May	Ads.	13	20.6
	September	?	7	18.0
Swamp Sparrow, <i>Melospiza georgiana</i>	October	?	1	15.8
	September	?	2	17.4

decrease again during the spring. Maximum differences between summer and winter months may amount to over 12 per cent. There is some unevenness in the weight variations from month to month in the case of individual species, but the significance of this must remain uncertain until more extensive data are obtained. The monthly fluctuations in weight of the Cowbird during the late spring and summer are opposite to those of other species and would be of special interest in connection with its parasitic reproductive habits, were it not that the number of records of adults of this species is rather few. Juvenal Cowbirds decrease in weight from June to August.

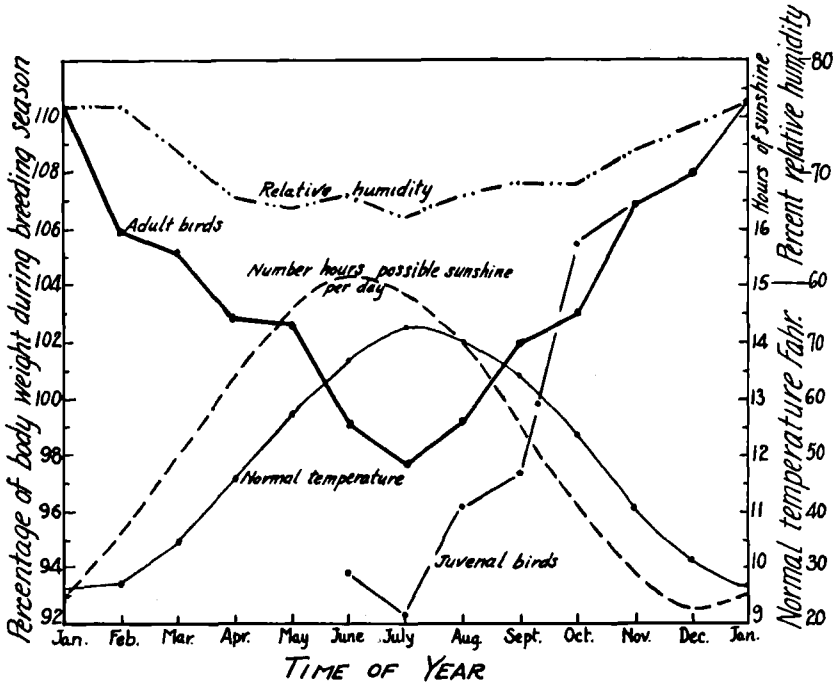
A study made of the monthly weight variations of individual birds shows that, while there are considerable, more random, fluctuations, the variation tendency evident in the above averages is also applicable to the individual. In other words, the monthly variations in the averages are not to be explained by chance combination of different individuals each month, but are due actually to weight changes in the individual, confirming similar studies of others.

A generalized curve based on monthly averages for all species is given in Text-fig. 4. Each month's weight is expressed in percentage of the average weight during the three principal breeding months of May, June, July. The conclusion appears warranted that adult birds of the species studied weigh, with some possible exceptions, more in the winter than they do in the summer.

Weight data on immature birds were prepared in the same way as were the data for adults. The average monthly weight of the immatures of each

species was divided by the standard breeding weight of the adult, to give a percentage figure. The data for all species were then averaged and plotted (Text-fig. 4).

In general, during the breeding season the juvenal birds weigh less than the adults, although by September or October they equal or surpass them. Text-fig. 4 indicates that during October the young birds may average more than the adults, but this may be an insignificant random variation.



TEXT-FIG. 4.—Average annual rhythm in weight of wild birds together with annual rhythm of various environmental factors.

In some species that breed farther to the north, immatures continue to weigh less than the adults in October, viz., White-throated Sparrow, White-crowned Sparrow and Slate-colored Junco. The rapid rise in body weight from July to October is even more pronounced in the immatures than in the adults, 13.1 per cent compared with 5.2 per cent. One might argue that this increase in weight of the immatures was due to the age factor, the birds becoming heavier as they grew older, were it not that there was also an increase in the weight of adult birds at the same time. However, the difference in the percentages of increase during these months is probably due to the maturing of the younger birds.

The possible explanation of these monthly variations in weight throughout the year is one of interest. The fact that even the juvenals weigh less in July than in June would indicate that the variations are not to be explained as due only to effects of reproductive activities, such as the feeding of the young. Partin (1933) also found that juvenal House Finches dropped in weight during midsummer, as they weighed more during May than in either June or July. This could hardly be due to the adaptation of the young to their own support, as he claims, for the older they get the more proficient they should become in finding food. The uniformity of the change from January to July and back again to January seems to imply some constant influencing factor that itself varies in a similar manner.

One factor that first suggests itself is the amount of available food. A quantitative estimation of the amount of food available each month is not possible but presumably it would be greatest in summer and early autumn and least in winter and early spring—yet the bird's weight varies in the direction opposite to what one would expect if the amount of food were the only important factor. Precipitation, as rain during the warmer months and snow during the colder months, varies little from month to month. Normal precipitation for the Cleveland, Ohio, region averages least in December and April (2.44 inches) and most in July (3.45 inches). The small difference between the extremes is not sufficient to suggest any direct or indirect effect on bird weight.

Monthly variations in normal temperature, normal relative humidity, and possible hours of sunshine per day are plotted in Text-fig. 4. Number of possible hours of sunshine per day varies from month to month in an inverse manner to the weight variations, but the extremes in these two curves do not exactly coincide. The number of hours of sunshine does not appear to be the important factor in causing weight variations, since if this were true one would expect a positive correlation, not an inverse one. With the longer days for feeding and the shorter warmer nights of summer the bird's weight should increase rather than decrease. There is a positive correlation existing between monthly variations in relative humidity and weight. Such a correlation would be important if there were reason to believe that differences in humidity affected body weight to any appreciable extent as by influencing the loss of water from the body. The experimental evidence for this is small, and temperature seems to affect this water loss from the body to a much more striking degree than does humidity (Kendeigh, 1934). One is hardly justified in suspecting that the difference of 10 per cent between the extreme monthly average humidities exerts any such great influence. The curve of normal monthly air temperature varies inversely with the curve of monthly weight. The extreme points in the two curves coincide as to the month in which they occur and the variation be-

tween the extremes is uniform in both cases. Presumably, the amount of temperature variation is also amply sufficient to affect body weight. Previous experimentation with passerine birds (Kendeigh, 1934) has demonstrated that weight loss is very responsive to variations in air temperature. One could logically expect some correlation between weight and temperature although at first one would expect a positive, rather than an inverse correlation. Other effects of temperature than merely on losses in weight must be involved, probably on weight gains during the daytime, if this inverse correlation is to be substantiated.

INFLUENCE OF TEMPERATURE ON VARIATION IN WEIGHT

Linsdale and Sumner (1934a) have studied the influence of temperature on weight changes with four Golden-crowned Sparrows kept in captivity and weighed several times a day for about two months in the spring. They found that ". . . all four birds showed increases on the same days and decreases on the same days. These simultaneous changes in one direction occur too often to be the result of chance. Some one external factor seems to have influenced the weight of these birds much more markedly than any others. From field observations of the behavior of this species, we suspected that weather records might furnish a clue to the explanation. Comparison of curves of weights and of weather records reveals that every well marked drop in weight was coincident with or within a day or two after a day of especially high temperature. Conversely all four birds tended to gain weight during cool weather. Preliminary tables of correlation suggest that the highest negative correlation of weight records is with the maximum temperature reading of two days previously. . . . Possibly the heat of late spring days may have some influence upon time of departure of this species for its northern breeding grounds." Hicks (1934) states that Starlings commonly gain weight in cold weather but may lose considerable weight during extreme cold. When weight is thus lost it may be regained during succeeding warm weather. In a recent study, Mrs. Nice (1938) found that White-throated Sparrows weighed less in the mild autumn of 1931 than in the cold autumn of 1932.

In order to determine in this study the possible effect of variations in air temperature on the weight of birds, average bird weights for individual days were compared with the average air temperatures. The first difficulty in working out this comparison arose in the determination of the proper period in which to average the air temperatures. Is the average weight of a bird during the day a response to the air temperature that same day or for a preceding period of time? Since the daily rhythm in body weight of these small birds is so marked, the body weight would seem greatly affected by conditions influencing both weight loss, especially during the preceding

night, and weight gain, through the amount of feeding during the daylight hours. In attacking this problem, use was made of the greater amount of available weight data for adult Chipping Sparrows and immature Song Sparrows. Averages were made of all the weights obtained of these species for all the days on which seven or more weights were available. In order to eliminate as far as possible any influence of time of day at which the weights were obtained, averages were made only for days when at least one-fourth of the weights were obtained during the other half of the day than the remaining three-fourths of the weights. Average air temperatures were computed from the Cleveland Weather Bureau records for the same day on which the weight averages were obtained, for the preceding night, for the same day and preceding night, and for the same day and preceding day. The temperature for a day is the average (really the median) of the maximum and minimum temperatures recorded during the twenty-four hours. The minimum temperature usually occurs near daybreak, the maximum usually in early or mid-afternoon. The night temperature was computed by averaging the mean temperature of the preceding day (a temperature which is usually actually attained about 8.00 p.m.) and the minimum temperature of the day following.

TABLE 6
*Correlation between Average Daily Weight and Average Air Temperature over
Different Periods of Time*

Period of time	Adult Chipping Sparrows			Immature Song Sparrows		
	Coefficient of correlation ¹	Standard deviation	Coefficient divided by deviation	Coefficient of correlation	Standard deviation	Coefficient divided by deviation
Same day	-.456	±.096	4.8	-.177	±.114	1.6
Preceding night	-.423	±.100	4.2	-.134	±.116	1.2
Same day and preceding night	-.422	±.100	4.2	-.130	±.116	1.1
Same day and preceding day	-.434	±.098	4.4	-.147	±.115	1.3

Data were available for sixty-eight days for the adult Chipping Sparrows and for seventy-two days for the immature Song Sparrows. Coefficients of correlation were computed between average daily bird weight and the average temperature during each of the periods mentioned above and are given in Table 6. In all cases an inverse correlation between body weight and air temperature is evident, i.e., the bird's weight increases with drop in air temperature, and vice versa. The correlation is good in the adult Chipping Sparrows but small in the immature Song Sparrows. With the

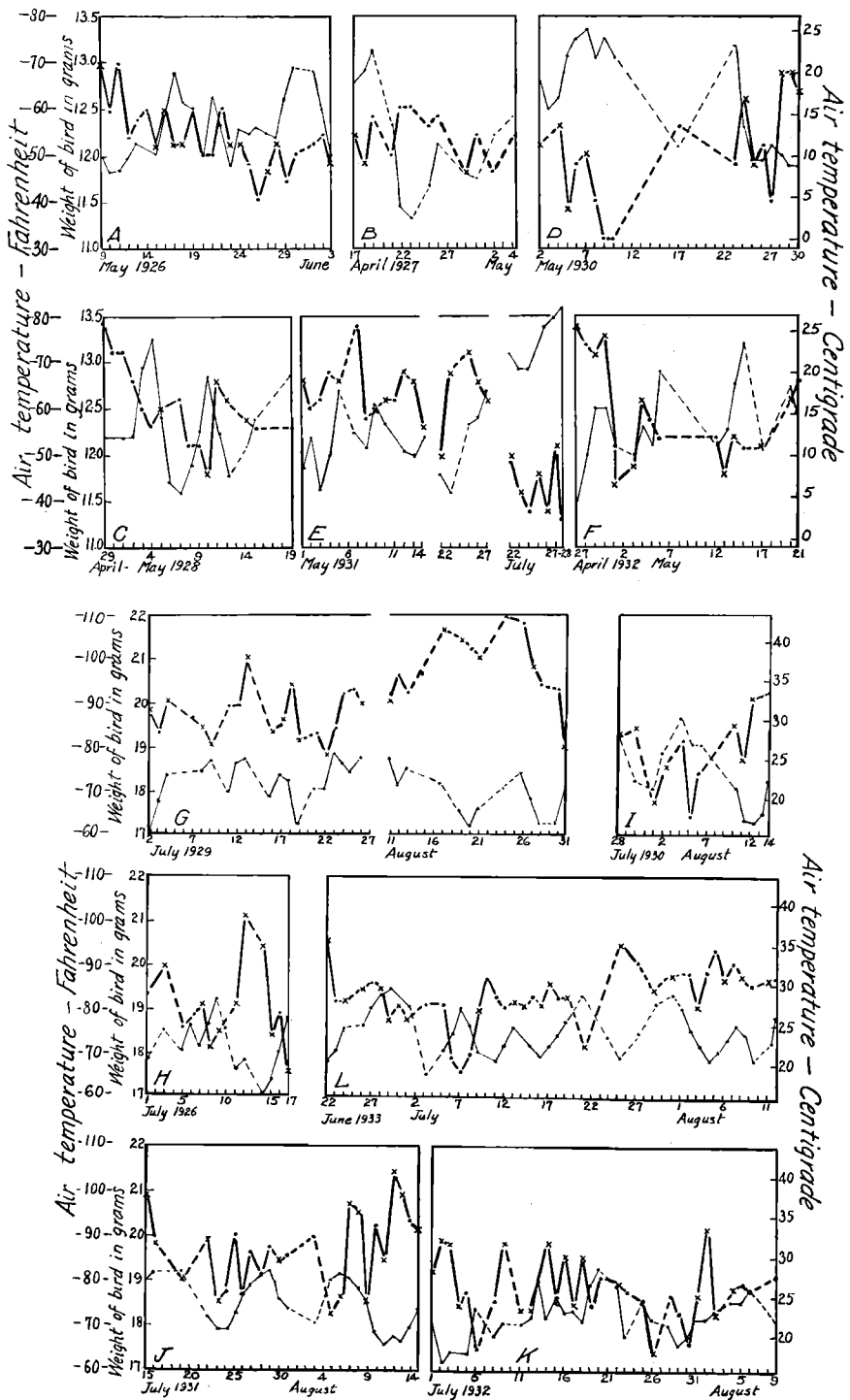
¹ A perfect positive correlation would give a coefficient of +1.0; a perfect negative correlation, -1.0; no correlation at all, 0.0.

Chipping Sparrow the correlation is very reliable, but with the Song Sparrow it is much less so. A coefficient equal to the standard error gives a percentage probability of only 68 that the correlation is not due to chance, two times the standard error raises this probability to 95, while three or more times the standard error makes it relatively certain with a percentage probability of 99.7 or better. The highest and most reliable correlation in case of both species is with the mean air temperature of the same day. Actually this mean daily temperature is approximately the average temperature for the daylight hours from daybreak until the middle afternoon, the actual time when most of the weight data were obtained. Taking the average temperature for the same and preceding days lowers the degree of correlation, but not so much as does the average night temperature. The data indicate that for further analysis of bird weights the best correlation would be with the air temperature during the same day.

A coefficient of correlation was calculated for average daily weight of adult Chipping Sparrows of both sexes and the average relative humidity on the same days. This proved to be $+ .214 \pm .116$, the coefficient being 1.8 times the standard error. Suspecting that this positive correlation with relative humidity may be a reflection of the temperature factor, since relative humidity often varies with temperature, we worked out a coefficient of correlation between the relative humidity and the temperature on the same days. This turned out to be $- .375 \pm .103$ (coefficient being 3.6 times the standard error). Thus, the positive correlation with relative humidity is probably due to both it and the bird's weight being inversely correlated with air temperature.

The next step was to study the day by day variation in body weight in response to the daily variation in average air temperature. The data for the above two species are plotted in Text-fig. 5. Weights of other species are not sufficiently numerous or suitable for this sort of analysis. It will be at once noticed that the general trends of the weight and temperature curves in the case of the adult Chipping Sparrow are inverse to each other. With the immature Song Sparrows the inverse relationship is much less apparent, although here and there it may be discerned. An age factor may be involved with this species not only because all the weights are for immature birds but also because the birds caught on different days may vary considerably in the length of time that they have been out of the nest. Still another consideration here is that the study with the Song Sparrow is for the midsummer months with their generally high air temperatures, while for the Chipping Sparrow the time involved is principally the cooler month of May during which the birds may be more responsive.

An intimate study of the charts for the Chipping Sparrow shows that the inverse correlation between weight and air temperature does not hold con-



TEXT-FIG. 5.—Day-by-day variations in weight of wild birds together with mean temperature on the same days. A-F, Chipping Sparrow; G-L, immature Song Sparrow. Heavy line—variations in the weight of the birds. Dots in heavy line—record for day being average of seven or more properly distributed weights. Crosses in heavy line—record for day being average of three to six weights only or where weights were irregularly distributed during the day; averages for these days are included only when supported by similar records on adjacent days. Light line—mean daily air temperature.

sistently true day after day. This may be due to an inadequate number of weight data for certain days, to other complicating factors, to the fact that the weight of a bird may not be responsive to small variations in temperature, or to the possibility that the correlation between weight and temperature is not such that if the data were plotted a perfectly straight line would result. Perhaps all these modifying factors are important; nevertheless, the general inverse trends in the fluctuations of these factors over shorter or longer periods of time are evident. This day by day inverse correlation between weight and temperature confirms what was similarly brought out by Linsdale and Sumner (1934a) for the Golden-crowned Sparrow.

The next step in the correlation involved the sorting out of the average daily weights of birds into groups falling within separate five-degree ranges of mean daily temperature so that the average body weight in each range of temperatures could be compared with the average air temperature for each range (Table 7). Although in some instances the number of records is not sufficient to eliminate minor fluctuations, in general, the inverse relation between mean body weight and temperature is conspicuous. The standard deviations are rather large so that the correlation is not as reliable as one might desire. Probably one reason for this is that, in order to include a sufficient volume of records over a wide range of temperatures, average weights for days are included when as few as three weights were obtained, except in the adult Chipping Sparrows and immature Song Sparrows where average weights are included for no days with less than seven weights. Statistically, the inverse correlation has significance in most cases when the average weights at the two extreme temperatures are compared (Arkin and Colton, 1934, p. 113). The differences between these weights, when compared with the standard error of this difference are: 6.2 times in the Tree Sparrow; 4.6 times in the adult Song Sparrows; 4.1 times in the Chipping Sparrow; 3.0 times in the English Sparrow; 1.5 times in the immature Song Sparrow; and 0.8 times in the White-throated Sparrow. It is to be recalled that differences between means are of high statistical significance when they are three or more times their standard error. On this basis, the correlation between temperature and weight is less certain in the immature Song Sparrows and the White-throated Sparrows but fully significant in the other species. With the immature Song Sparrows this may be due to reasons already mentioned. With the White-throated Sparrow, the correlation becomes of greater significance (2.7 times) when the average weights are compared at temperatures 43° and 72° F. (6.1° and 22.2° C.) instead of at 38° and 72° F. (3.3° and 22.2° C.).

When the coefficients of variability of weight in each temperature range were computed (by dividing average standard deviation by average body weight) and averaged, it was found that the species ranked from least

TABLE 7

Statistical Correlation between Bird Weights and Air Temperature

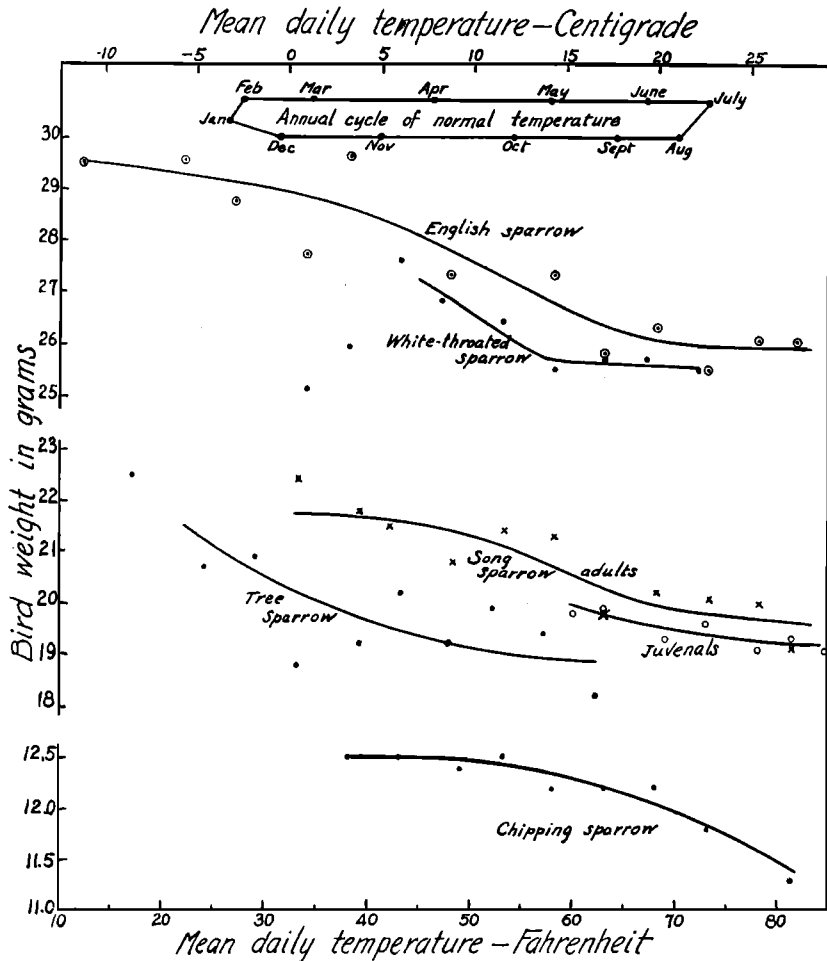
Average air temperature	Number of days' records	Average weight	Standard deviation
Song Sparrow—adult male			
33° F. + 0.5° C.	1	21.3 gms.	—
40 + 4.4	4	21.6	1.25 gms.
42 + 5.5	5	21.7	0.92
49 + 9.4	3	21.1	1.18
53 +11.6	4	21.5	0.73
58 +14.4	4	20.8	1.06
63 +17.2	3	20.0	0.35
68 +20.0	2	21.1	1.40
73 +22.7	2	20.4	0.85
78 +25.5	4	20.4	0.29
Song Sparrow—adult female			
40° F. + 4.4° C.	1	21.0 gms.	—
48 + 8.8	3	19.5	0.66 gms.
53 +11.6	3	21.0	1.18
58 +14.4	3	20.9	1.30
62 +16.2	2	19.0	1.70
67 +19.4	2	18.6	0.30
72 +22.2	2	19.4	0.85
77 +25.0	3	19.8	0.69
Song Sparrow—all adults regardless of sex			
33° F. + 0.5° C.	8	22.4 gms.	1.14 gms.
39 + 3.8	19	21.8	1.01
42 + 5.5	9	21.5	0.95
48 + 8.8	15	20.8	0.99
53 +11.6	24	21.4	0.94
58 +14.4	16	21.3	0.71
63 +17.2	14	19.8	1.27
68 +20.0	22	20.2	1.00
73 +22.7	17	20.1	0.76
78 +25.5	8	20.0	0.59
82 +27.7	5	19.2	1.26
Song Sparrow—immatures			
60° F. +15.5° C.	1	19.8 gms.	—
63 +17.2	6	19.9	0.84 gms.
69 +20.5	23	19.3	0.70
73 +22.7	17	19.6	1.02
78 +25.5	17	19.1	0.85
82 +27.7	7	19.3	0.52
86 +30.0	1	19.1	—

TABLE 7—(Continued)

Statistical Correlation between Bird Weights and Air Temperature

Average air temperature	Number of days' records	Average weight	Standard deviation
Chipping Sparrow—adults			
38° F. + 3.3° C.	1	12.5 gms.	—
43 + 6.1	3	12.5	0.14 gms.
49 + 9.4	9	12.4	0.46
53 +11.6	19	12.5	0.46
58 +14.4	11	12.2	0.32
63 +17.2	4	12.2	0.35
68 +20.0	11	12.2	0.32
73 +22.7	9	11.8	0.45
82 +27.7	1	11.3	—
English Sparrow—all records			
12° F. -11.1° C.	1	29.5 gms.	—
22 - 5.5	2	29.6	1.50 gms.
27 - 2.7	3	28.8	0.48
34 + 1.1	1	27.8	—
38 + 3.3	3	29.7	0.78
48 + 8.8	2	27.4	2.80
58 +14.4	2	27.4	1.65
63 +17.2	7	25.9	1.24
68 +20.0	16	26.4	1.61
73 +22.7	9	25.6	1.57
78 +25.5	15	26.3	1.67
82 +27.7	10	26.2	1.27
White-throated Sparrow—all records			
34° F. + 1.1° C.	1	25.2 gms.	—
38 + 3.3	4	26.0	0.64 gms.
43 + 6.1	4	27.7	1.35
47 + 8.3	9	26.9	1.15
53 +11.6	10	26.5	1.06
58 +14.4	21	25.6	1.14
63 +17.2	16	25.8	1.60
67 +19.4	5	25.8	0.98
72 +22.2	5	25.6	0.89
Tree Sparrow—all records			
17° F. - 8.3° C.	1	22.5 gms.	—
24 - 4.4	2	20.7	0.50 gms.
29 - 1.6	3	20.9	0.53
33 + 0.5	5	18.8	0.58
39 + 3.8	14	19.2	0.68
43 + 6.1	6	20.2	0.72
47 + 8.3	4	19.2	1.31
52 +11.1	9	19.9	0.55
57 +13.8	5	19.4	0.80
62 +16.6	2	18.2	0.25

variable to most variable as follows: Chipping Sparrow (2.9 per cent), Tree Sparrow (3.4), immature Song Sparrow (4.1), adult male Song Sparrow (4.2), White-throated Sparrow (4.2), adult female Song Sparrow (4.8),



TEXT-FIG. 6.—Relation between average daily bird weight and mean daily air temperature.

and English Sparrow (5.3). With the exception of the adult female Song Sparrows, this order of increasing variability of weight corresponds with increasing average weight of the birds, rather than with decreasing weight as Groebbel (1932) maintains. However, this subject needs further special study.

A few individual birds have repeated to the traps a sufficient number of

times to permit some study of their individual daily weight fluctuations compared with temperature. In spite of considerable random variation, a tendency toward inverse correlation between the two factors was evident.

The data in Table 7, when plotted, exhibit some interesting relations (Text-fig. 6). The first striking feature that is obvious in this figure is that the relation between bird weight and air temperature is not to be depicted as a straight line, at least over all ranges of temperature. Rather, the relation is better expressed by a curve which may be either concave or convex. Records are available for the English Sparrow and adult Song Sparrow over a wider range of temperatures than for any of the other species. From these more nearly complete series of data, it is apparent that the curve at higher temperatures is concave while at lower temperatures it is convex, really an inverted sigmoid curve. The curves for the other species appear to be fragments of sigmoid curves which would be completed if records were available over a wider range of temperatures. For the White-throated Sparrow and the Tree Sparrow, the curves appear to represent the lower part of a sigmoid; for the Chipping Sparrow, the upper part. These sigmoid curves appear to be approaching upper and lower asymptotes, that is, there appear to be upper and lower limits in variation of weight over the normally tolerated range of temperatures. These limits are different for the different species concerned.

The relation between body weight and air temperature is of considerable interest in the physiological ecology of birds. In a previous study (Kendeigh, 1934) experiments showed that heavier birds have a greater resistance than do lighter birds to low temperature over a period when obtaining food is difficult, since this extra weight is mostly fat. This fat is utilized to maintain the higher rate of metabolism at these lower temperatures. At high air temperatures the reverse is true. Lighter birds generally have a greater resistance to heat, since the proportion of their body surface area (internal and external) to body mass is greater, and surplus body heat may be dissipated more rapidly.

If the bird's weight is capable of only a limited amount of increase or decrease as a response to temperature, this factor may be of significance in affecting its temperature tolerance, consequently its distribution, migration, and abundance. For instance, if the temperature becomes very low, going beyond the maximum limit of adjustment, the bird's weight may drop, as shown by Hicks (*loc. cit.*), and if continued, may result in the death of the bird.

Of this group of species studied (Text-fig. 6), the Tree Sparrow appears to have the greatest possibility for weight increase with further drop in temperature although its curve is drawn with a considerable degree of uncertainty. It has the most northern distribution during both the breeding

and the wintering seasons, according to the A. O. U. 'Check-list' (1931 edition). Likewise, this species reaches its lower limit of weight decrease at the high temperature that is least extreme, and so appears least resistant to high air temperature. Its southern limit of distribution is farther to the north than that of any other species in this group. If the two lowest records in the range from 30° to 40° F. (-1.1° to 5.6° C.) for the White-throated Sparrow are disregarded, since they are based on averages for only five days in all, this species appears also to be highly tolerant of low temperature, since the curve does not flatten out, and next least tolerant of high temperature. It is distributed not quite so far north as the Tree Sparrow and occurs farther to the south in the summer. Likewise, it winters farther south. The English Sparrow is more tolerant of high air temperature than either of the two species above discussed and correspondingly occurs farther south during the breeding season. Due to the wide scattering of points the exact tolerance of low temperature can only be approximated. Apparently it is less than that of the Tree Sparrow which would agree with its less extensive northern distribution. From the data available one cannot say whether it is more or less tolerant of low air temperature than the White-throated Sparrow. The curve for the Song Sparrow is not drawn with any great certainty, but this species appears to be less tolerant of cold than any of the above-mentioned species, nor is it distributed quite so far north in the breeding season. Its tolerance of heat is about the same as that of the English Sparrow, which is out of harmony with the latter introduced species' more southern extension. The Chipping Sparrow appears the least tolerant of low air temperature and the most tolerant of high air temperature. It does not extend as far north during the breeding season as any of the other species and extends farther south than any species here in question, except, perhaps, the English Sparrow. Likewise, it winters farthest to the south, except for the English Sparrow.

Concerning the migratory status of these species in northern Ohio, the English Sparrow is a permanent resident, apparently better fitted than any other species for the range of temperatures throughout the year in this region. Comparing its curve with the yearly cycle of normal monthly temperatures shows that the steepest part of the curve, where the bird's weight is most responsive to changes in air temperature, covers almost as extensive a range in temperature as does the cycle of normal temperatures. In other words the upper and lower limits of weight adjustment are barely reached under normal conditions. The same general relation holds for the Song Sparrow, except that during the winter the curve reaches its upper limit of weight adjustment sooner. The largest proportion, by far, of the Song Sparrow population migrates south in the autumn and avoids these mid-winter temperatures, but a few hardy individuals remain. With the

White-throated Sparrow and the Tree Sparrow, it seems that they do not remain to breed because of inability to become adjusted to higher air temperatures than those that normally occur in May. The Tree Sparrow regularly winters and the White-throated Sparrow rarely does. The weight-temperature curve shows that the Tree Sparrow is fully capable of so doing. The curve for the White-throated Sparrow is inconclusive but this species may be fully capable of remaining over winter as far as temperature tolerance is concerned. That it does not do so may mean that in this case other factors, such as possibly food, may be more important. The Chipping Sparrow in this region approaches the upper limit of its weight adjustability during the breeding season, so it occurs only during the open summer season and migrates south in the autumn so that none winter this far north. In the case of all species, individual birds may occasionally show special weight-temperature adjustments that permit them to remain in regions to which the majority are not adapted.

Differences in the regional abundance of a species may be due to differences in the air temperature of those regions in relation to these weight-temperature adjustments. Likewise, differences in yearly abundance of a species may be correlated with yearly temperatures approaching or surpassing the upper or lower limits represented by weight adjustability.

DISCUSSION

A surprisingly large number of records of the weight of birds is required before reliable interpretations can be made. Aside from individual variations, sex, age, time of day, season, and temperature all produce fluctuations, and so in order to study the effect of any one factor allowance for all other factors must be made. Much of the discrepancy that occurs in the results of different investigators or of the same investigator with different species may be due to the insufficient number of records available.

Little attention was paid in this study to differences in weight of individual birds, largely on account of the considerable difficulty of obtaining a sufficient number of records of individual birds over a wide enough variety of conditions to make such a study significant. Individual differences undoubtedly do occur which are ingrained, as with other characteristics of the bird, in their hereditary constitution and in the conditions of their development.

Sex and age differences in weight are noted in the case of certain species. The significance of weight differences between the sexes may be hidden in their phylogenetic development and is not as obvious in the present adjustment of the sexes to their environment as one might wish. Age differences in weight are, of course, correlated with the problem of development, and

further discussion of this point may be deferred for a more extensive treatment of that problem.

The daily rhythm in body weight seems, at least in small passerine birds, not to be the simple matter of emptying the digestive tract at night and filling it again during the daytime, as is commonly supposed. This may, however, account for some of the differences between early-morning weights and those obtained later in the day. The digestive tract contains food probably amounting to less than 5 per cent of the body weight in small passerine species. In forms with crops the percentage will of course be larger. Experiments with passerine species (Stevenson, 1933) have shown that one and one-half to two hours is a long enough time to permit a small bird to fill again its digestive tract and begin egestion, and that birds as a rule maintain a moderately full stomach at all times—not alternately emptying and filling it to capacity as might be supposed. Thus, in the early morning hours intensive feeding may quickly replace the contents of the digestive tract lost during the preceding night. In the present study, very few weights were obtained before 7.00 or 8.00 o'clock in the morning, two or three hours after the beginning of early-morning feeding. Thus, the 5 to 6 per cent difference that was noted between maximum and minimum average hourly weights after the early-morning feeding period was well begun must be due in large measure to other factors.

No experimental analysis of what these other factors may be has been made, although certain theoretical points may be mentioned. In the metabolism of recently active and feeding birds Benedict and Riddle (1929) and others obtain respiratory quotients of 1.0 or thereabouts, which means that the carbohydrates furnish the chief source of energy and indicates that by volume the carbon dioxide loss equals the oxygen absorption. Between twenty and twenty-four (sometimes fewer) hours without food are required for pigeons and doves (which have crops) to lower their respiratory quotients from 1.0 to 0.7; the latter figure indicates that the birds are metabolizing body fat. Such birds would not ordinarily reach this condition during any night, since the number of hours of darkness during the winter may be fifteen and during the summer only nine. It appears, therefore, that the daily rhythm of birds with sizeable crops is more nearly a matter of filling and emptying this reservoir of stored food than in small birds lacking crops, although even in large birds part of the loss at night must be due to utilization of body resources.

For small passerine birds without crops, emptying of the alimentary tract of food during the daytime may be accomplished in about two and one-half hours. Possibly at night a longer time is required, but when this is completed, metabolism must gradually shift from a carbohydrate to a fat basis. Benedict and Fox (1933) found that canaries and English Sparrows

reach such basal or fat metabolism within ten to twelve hours. Out-of-doors and exposed to lower air temperatures, it is quite likely that fat metabolism is reached much sooner, and is probably reached every night. Baldwin and Kendeigh (1932) found that 4.7 hours was a sufficient period for House Wrens to reach basal or standard metabolic conditions, if the obtaining of their standard body temperature may be taken as evidence. With a respiratory quotient of 0.7 the weight difference between the carbon-dioxide output and oxygen intake is approximately equal. Loss of weight would be principally of water and excrement. The importance of water imbibition and loss in the daily rhythm is not known.

There is thus reason to believe that the daily rhythm in body weight of small passerine birds, such as are here studied, means not merely the emptying and filling of the digestive tract but actually an extensive utilization of stored carbohydrates and fats during the night and their replacement during the daytime. The metabolism of these small birds is so great in proportion to their bulk and their ability to store reserve food in their bodies is so limited that they live within a very narrow margin of safety and are highly responsive to variations in environmental conditions. This responsiveness to the environment is well defined in the correlations made between body weight and air temperature. At lower temperatures (unless extreme) there is not, as one might suppose, a drop in average daily weight, but rather an increase. The drop in weight at night is probably greater because with lower temperature there is an increase in the rate of metabolism and consequent utilization of reserve body supplies of carbohydrates and fats. During the following daytime, however, this increased loss is apparently more than made up by an increase in the amount of feeding. Since the coefficient of correlation between variation in weight and the preceding night temperatures ($-.423$) is almost as high as the coefficient using the temperature of the same day ($-.456$), it would seem that the primary stimulus for increased feeding may lie somehow in the loss or in the losing of the weight itself, a stimulus which is carried over into the following day. However, the low temperature may have some direct stimulating value in itself, as well, since the coefficient using temperature of the same day is even higher than that for the preceding night, and during the day there is no loss in weight.

That birds actually do feed more on cooler days has been shown by Stevenson (1933) who found that about twice as many sparrows were caught in banding traps, where they had come for food, on days with air temperatures averaging 71° - 75° F. (21.7° - 23.9° C.) than on days with air temperatures averaging 81° - 85° F. (27.2° - 29.4° C.). Mr. William H. Long of the University of Michigan has kindly consented to the inclusion here of some of his unpublished data on game birds that show the same relation between feeding

and air temperature. In the winter of 1935-36, during a period of seventy-three consecutive days with temperatures around or below freezing and including fifteen days below 0° F. (-17.8° C.), fourteen adult Bob-whites consumed on an average 1.72 grams per hour per bird or 17.2 grams for the ten-hour day. Six birds, held during the same period as controls at a temperature of 72° F. (22.2° C.), consumed on an average 1.29 grams per hour per bird or 12.9 grams for the day. Ten birds of the same species, during a period of excessive heat during the summer of 1936 when the temperature did not fall below 70° F. (21.1° C.) and at one time reached 104° F. (40.0° C.), consumed on an average 0.62 grams per hour per bird or 9.24 grams for the fifteen-hour day. A pair of Ring-necked Pheasants (*Phasianus colchicus torquatus*), during the same two periods above mentioned, consumed, during the winter period, 5.94 grams per hour per bird or 59.4 grams per day and, during the summer period, 1.47 grams per hour per bird or 22.0 grams per day. During periods of severe cold in winter, some species may temporarily refrain from feeding in order to linger in protected shelters or huddle with other individuals to conserve body heat.

The apparent over-compensation, by increased feeding, of the weight lost during the preceding night is an efficient safety factor in the life of the bird, since it better prepares the bird to tolerate unfavorable weather conditions to come. There is, nevertheless, a limit to this possibility of adjustment. If the temperature drops too low or endures too long, the bird may find itself during the daytime unable, by increased feeding, to make up the losses at night. It would then be necessary for the bird, in order to survive, to move into a more favorable environment. On the other hand, during days with high temperature, there should be less loss of weight at night. During the following daylight period, there should then be less need for feeding. The amount of feeding may, under these conditions, be so far reduced as actually not to make up for the weight lost during the preceding night.

Reduced feeding may be correlated with generally reduced activity as temperatures are raised. Mr. William H. Long has compiled for July and August over a period of four years some five thousand individual observations of the amount of activity displayed by birds in their natural habitats. He finds a very high negative correlation with temperature (-0.91 ± 0.016) and a lesser correlation with relative humidity. With reduced activity there is diminished metabolism and heat production, which is of decided benefit to the bird in hot weather. Whether or not the reduced feeding is the result of the generally reduced activity is a matter of importance but can only be speculated upon at the present time.

The yearly rhythm of weight is one of considerable interest. The increase in weight during the autumn and winter is marked. After the late-summer and early-autumn molt, the bird has the heaviest coat of feathers

during the entire year. This makes the weight loss when without food much less than at the same temperatures during the summer because it is equivalent to keeping the bird at a higher air temperature (Kendeigh, 1934). Their bodies are less exposed to air temperature than they were during the summer. Even though in the autumn, night temperatures are somewhat lower than in the summer, the birds apparently at first lose weight at night less rapidly. They may or may not respond to the lower temperatures during the daytime by increased feeding, but the food consumed appears more completely stored in their bodies as reserve. They thus increase in weight. The weight increase would be even greater except that the night time without food is becoming increasingly long and the temperatures increasingly low as the season progresses. Some species migrate out of the region before these temperatures become so extreme as to offset entirely the advantage of their heavier feathering. Permanent-resident species continue to tolerate these increasingly long cold nights and are ever able to feed sufficiently during the day to more than offset the losses at night except occasionally when very severe weather occurs. Without nesting cares or other drains on their vitality, they may devote a larger share of their time to feeding and are able to utilize their energies more completely to tolerate the winter conditions.

The decrease in the feather covering of the body that began at once after the autumn molt, reaches appreciable proportions by spring and becomes extensive by summer. This means that the body becomes more and more exposed to the effects of air temperatures, there is increased heat radiation from the body, metabolism is proportionately increased even at moderate air temperatures, and weight losses during periods without food go on at a faster rate. This is compensated, to a larger or smaller extent, by the rising air temperatures and decreasing number of hours of darkness, but joined with this increased rise in air temperature may be a reduced rate of feeding. It is not known whether the variation in rate of feeding is influenced directly through the temperature senses of the birds or indirectly through the changed metabolic conditions produced. The amount of feeding during the daytime may be further reduced by the obliged utilization of part of the time for carrying on courting and nesting activities. There is a demand for energy for the maturing of the ova and the spermatozoa as well as associated activities of singing, nest building, possibly incubation, and certainly the care of the young. The correlation between day by day fluctuations in weight and temperature would indicate that temperature must, however, be one of the important factors involved, probably even more important than reproductive activities. The composite effect of these various influences is a gradual weight reduction until mid-summer.

Molting and renewal of feathers in August and September is not joined with a decrease in weight; rather there is an increase in weight at that time. The possibility exists that weight changes may be also affected by variations in activity of the thyroid or other endocrine glands, which may be correlated with seasonal changes in the rate or type of metabolism. Such endocrine activity may in turn be related to changes in temperature, length of day, or other environmental influences. Some studies of seasonal changes in endocrine activities have already been made but are not advanced sufficiently to warrant extensive discussion at the present time.

This study of yearly rhythm in weight exposes interesting correlations with the migratory status and distribution of the various species. Limits of variations compatible with normal activity and comfort out-of-doors become apparent. These, presumably, represent limits of physiological adjustment to high and low air temperatures, and such limits of adjustment vary among permanent residents, winter visitors, summer breeders, and transients. Migration would appear not to be a stereotyped instinctive behavior based on internal rhythms alone, but instead is definitely related and probably dependent upon proper environmental influences for its release. Likewise, the reasons for the different ecological distribution of species within the same geographic region become more and more clear as further studies are made of the interrelations between physiological processes, their limits of variation, and environmental influences.

CONCLUSIONS

1. Differences occur between the weights of different individual birds but such differences are scarcely greater than may occur in the weight of a single individual at different times. The individual varies slightly less in its weight the more nearly it approaches the average weight of the species.

2. In nine out of twenty-four species studied to determine the effect of sex on body weight the two sexes were of nearly equal average weight, in eleven species the males were definitely heavier, and in four species the females were heavier. The accumulation of a greater volume of records may possibly change the relative status of the sexes in a few species in which the number of data now available is not great.

3. In general, juvenal birds weigh less than the adults during the summer. In many species this difference is erased by October, but in other species it persists longer.

4. There is a daily rhythm in the weight of the birds investigated, with the greatest weights being reached in late afternoon or early evening and the lowest weights early in the morning. The weight increases most rapidly during early morning, slows up during the middle of the day, and increases rapidly again during late afternoon and early evening. Periods of most

rapid weight increase correspond with periods of most active feeding. The extreme weight variation of the smaller passerine species during the day may amount to between 8 and 12 per cent of the mean daily weight but this may vary with differences in air temperature, amount of feeding, and other activities.

5. There is a yearly rhythm in the weight of the birds investigated with the greatest weights being reached usually in midwinter and the lowest weights usually in midsummer, and this is inversely correlated with monthly variations in temperature. Average monthly weights, differentiated as to sex and age, are given for eighty-five species on the basis of a total of 13,546 records.

6. There are day by day variations in the weight of birds correlated inversely with the average temperature especially for the same day.

7. The average daily weight of birds when plotted with average daily temperature shows an inverse sigmoid curve type of correlation, with a maximum weight limit being approached at low temperature and a minimum weight limit being approached at high temperature.

8. Differences in the weight-temperature curves and the points at which the limits of variation in weight consistent with normal health and vigor are reached occur among species and may be correlated with differences in their distribution and migratory status.

9. The manner and extent of fluctuations in weight give further evidence that birds in their physiological adjustments are highly sensitive to environmental influences, and that this interrelation between function and environment greatly affects their behavior.

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