WINTER AND MIGRATORY WEIGHT AND FAT FIELD STUDIES ON SOME NORTH AMERICAN BUNTINGS*

By CARL W. HELMS and WILLIAM H. DRURY, JR. **

GENERAL

From the discussion of bird migration by the Hohenstaufenkaiser Friedrich II in the thirteenth century to the present day, investigators have been interested in ranges and migratory routes of birds. This interest did not yield large scale results, however, until the initiation of various national banding programs around 1900. Today, ranges and migratory routes of many species are well known (cf. Steinbacher, 1951; Schüz, 1952; Lincoln, 1952).

It was discovered that different populations exhibit several types of seasonal movements, ranging from seasonal food wanderings varying from year to year in extent and intensity with the abundance of food, to innate fixed patterns of migratory movements which are largely independent of the environment. True migration is a periodic and oriented movement of at least a part of the population (Farner, 1955). However, study of the periodic and oriented nature of migration has been recent, and all migratory orientation studies such as Sauer's recent demonstration of star-orientation (1957) are dependent upon the bird's migratory drive; i.e., in order to study migratory orientation, the bird must be in a migratory condition. Thus, the periodic nature of migration is basic to understanding migration in general.

Study of the migratory condition in birds was initiated by Rowan (1925) who found that captive Slate-colored Juncos, *Junco hyemalis*, given added light each day in winter, could be induced to migrate earlier than unlighted controls. A premature recrudescence of the gonads was associated with the increased lighting. This action of increased photoperiod in winter months has been demonstrated for many other species (reviews by Bissonnette, 1937; Burger, 1949), and has led to theories attempting to explain the periodic attainment of migratory condition in terms of gonadal changes induced by changing photoperiod (review by Farner, 1955). Yet, the various light-gonadal hypotheses are inadequate, as are all other hypotheses based on the response of one endocrine system to the environment.

It seems well established that the annual cycle found in all birds, of which migration is a part in some birds, is based on an internal rhythm (Aschoff, 1955; Marshall, 1958). This annual rhythm is

*The term "bunting" as used in this paper refers to any emberizine finch, Family Emberizidae, Subfamily Emberizinae (Mayr and Greenway, 1956).
**Contribution from the Hatheway School of Conservation Education Number 11.

analagous to the daily rhythm in that its setting may be dependent on environmental "time-givers" (*Zeitgeber* of Aschoff). Very limited evidence also suggests that there is an overt persistent annual rhythm in absence of the environmental time-givers (Benoit, *et al.*, 1955 and 1956; Sauer, 1957; Miller, 1955; Chapin, 1954). Any functional relations between daily rhythms and annual rhythms remain unknown, although there are pronounced changes in daily rhythms during the annual cycle in nocturnal migrants (Wagner, 1930).

Many environmental stimuli are known to act as "time-givers" during the annual cycle, and include light, temperature, rain, food, suitable habitat, and inter-individual behavior (Marshall, 1958; Aschoff, 1955). It would be tempting to include star patterns in this list as Sauer's experiments with astronavigation (1957) and some limited unpublished data we possess might suggest. However, the celestial pattern would give an exact indication of season to the bird only if (1) he possessed an accurate chronometer, or internal clock, and (2) he knew his exact position at the times of observation. There is no doubt that the first condition is met (Bünning, 1958; Aschoff, 1958), but the second is speculative.

Light has received most attention of these factors, and Benoit (review 1950) has demonstrated its action on the pituitary. That the anterior pituitary responds to photoperiodic changes, and that this gland controls a multiplicity of physiological interactions indirectly through other endocrine glands is obvious. It is not obvious, however, how and why this gland responds, how these responses differ in migrants and non-migrants, and how endocrine changes are related to behavior changes. Until more is understood about the basic physiology of the annual cycle, theories relating the annual cycle and migration to environmental setting stimuli or time-givers and their action on the physiology of individual birds are doomed to inadequacy.

Although Salomonsen (1955) has pointed out several important evolutionary considerations based on winter and summer distributions and migratory pathways, the historical origins of periodic migration remain obscure.

With an interest in ecology, physiology and origin of seasonal migration, we have been studying the annual cycle of some North American buntings.

The Migratory Condition, Migratory Unrest, and Migration

A number of related physiological and endocrine changes accompany approaching migration and migration itself. These changes include increased food intake (hyperphagia) and fat deposition, changes in metabolism, a series of changes in endocrine balances and control of various body processes, and changes in behavior, including activity. Psychic changes are involved, probably partly as cause and partly as effect, but cannot be studied directly. This preparation brings the bird into a "migratory condition" (*Zugdisposition* of various German authors). This migratory condition, the net result of interacting environmental time-givers and the internal annual rhythm of the bird, leads to migration in the wild, or to migratory behavior in captivity. The expression or performance of migration may be stimulated or

inhibited from day to day by environmental changes, *e.g.*, tempera-
ture, cloudiness, inclement weather, etc. The migratory behavior of
captive birds (*Zugunruhe*) was first studied by Wagner (1930) who
found that nocturnal activity in caged nocturnal migrants parallels
migration in wild birds from the same population. This has been
verified by Merkel (1938), Palmgren (1944), and other authors, and
its use in studies of migration reviewed by Farner (1955).

Thus in intact birds, fat change, which is also reflected in changes in
body weight, provides one index of migratory condition, while migra-
tory unrest may be used as an index to migration itself. We decided
to use these two indices in the general study of which this paper is a
part.

There is often misunderstanding between field and laboratory work-
ers, on the one hand as to the interpretation and control of variables
in field studies, and on the other hand, to the applicability of laboratory
results to field behavior. It is possible to obtain large samples of birds
in the field and to determine migratory condition, although migration
of individuals may be studied at only one point in space and time.
Migratory behavior can be observed continuously under laboratory
conditions where the retention of large samples to determine migratory
condition is impractical. Therefore, we decided to follow fat and
weight changes in wintering and migrant buntings in the field in
connection with our laboratory experiments on migratory unrest.

INTRODUCTION

The variability of bird weight from individual to individual, from
day to day, and during the day, led early collectors and banders
frequently to omit weight data. They relied on linear measurements as
indicators of body size. Valid and important as linear measurements
are, they cannot reflect physiological adjustments of birds during
the day and through the seasons. Raw mean weights are subject to the
same criticism. Statistical analysis, however, and the large numbers
of birds handled by banders at all seasons, make careful studies of
variation possible and important. Nice (1938) attempted to show
banders the usefulness of such data, which had been recognized by
Heinroth as early as 1922 (Heinroth, 1922). Baldwin and Kendeigh
(1938) and Hagen (1942) have analyzed many weight data for many
species and reviewed the main patterns of variation as we now under-
stand them.

In general, weight increases during the day. Most rapid increases
are found in the early daylight hours, rising to a peak or leveling off
during mid-morning hours. This may be followed by a drop in weight
or by a more gradual rate of increasing weight during mid-day hours.
Weight increases again during the early afternoon hours to the highest
weight of the day which comes in the mid-afternoon hours to sunset,
depending on the species. This diurnal weight increase represents in
part a balance between 1) ingestion of food, water and undigestible
matter, and excretion of waste, water loss, and the use of food for
energy; and 2) the storage of digested food in the body largely as
stored fat. Nocturnal weight loss represents excretion of waste, water
loss and energy utilization from stored reserves.

Baldwin and Kendeigh (1938) noted that seasonal changes in weight are inversely correlated with temperature, so that weight is highest in winter and lowest in summer. Nice (1938) gives several apparent exceptions to this pattern, *e.g.*, American titmice. However, Haftorn (1951), Kluijver (1952), and Owen (1954) have found seasonal variation in European tits, and recently, this pattern has been substantiated in the Black-capped Chickadee, *Parus atricapillus* (Lawrence, 1958). This variation is largely due to increased reserves of stored fat present in winter.

Female birds gain weight during the breeding season due to the rapid growth of ovarian folicles and oviducts prior to egg laying. Male gonadal growth is more gradual and the increase in weight of reproductive organs less than that in the female. Because the gonads are at or near the winter minimum and changes are small during the periods covered by this study, they will be neglected in considering sources of weight variation.

Seasonal low weights are associated with feeding young and the early part of post-nuptial molt.

In many small passerines, weight and fat increase during migratory periods in migratory populations.

Extreme weather conditions at any season may, if prolonged, affect both seasonal and daily weight and fat variation adversely. Prolonged snow cover in winter or rainy periods in summer primarily affect the food supply and not the bird directly (*cf. e.g.*, Haftorn, 1951).

The association of weight variation with changes in subcutaneous and visceral fat was established early. Naumann noted fat deposits associated with migration in the early nineteenth century (Farner, 1955). Heinroth (1922) proposed a scale of fat classification, which was expanded by Hagen (1942) to include degrees of fat not found in passerines. Wolfson (1942, 1945) and Blanchard (1941), however, were the first in this country to associate fat with weight increase, using the technique of McCabe (1943) which permits an objective rating of stored lipid in the intact bird. Odum (1949) used this technique in an analysis of fat and weight in relation to winter temperatures and spring migration in the White-throated Sparrow, *Zonotrichia albicollis*. Odum and Perkinson (1951) showed that subcutaneous fat deposits, especially those in the abdominal region, closely parallel total body lipids as analyzed quantitatively by extraction. Wolfson (1954, a,b,) established the statistical validity of his fat scale as representing significant weight increments. As the storage of glycogen (carbohydrate energy reserve) is limited and the bird can indulge in protein katabolism for energy supply to only a limited extent, determination of subcutaneous lipid deposits is a valuable indication of energy reserves available to the bird for survival in winter and to supply energy for migratory flight during migration. We hope banders will be encouraged to make observations of body fat on all birds handled.

Although fat reserves and food in the gut are the primary sources of weight variation during the day and year,there are several contributing sources. Oakeson (1953) found variations in liver and spleen weights in White-crowned Sparrows, *Zonotrichia leucophyrs*, amount-

ing to less than 1% and 0.2% of the mean body weight respectively. The highest weight occurred during spring migration. Fisher and Bartlett (1957) have described diurnal weight changes in livers of Red-winged Blackbirds, *Agelaius phoeniceus,* amounting to 2% of the body weight with highest weights in the late evening. Although important, these changes are small, relatively constant, and probably represent increased energy stores paralleled in fat deposition. We will neglect these changes and other potential factors which are insignificant in relation to body weight during the study period in the remainder of the paper.

METHODS

During the winters of 1956-57 and 1957-58, we spent more than one hundred days trapping and observing Tree Sparrows, *Spizella arborea,* and Slate-colored Juncos, *Junco hyemalis,* on the Drumlin Farm Wildlife Sanctuary, Massachusetts Audubon Society, South Lincoln, Massachusetts. This report is based on observations of 477 individual Tree Sparrows and 572 Slate-colored Juncos, with over 2000 handlings of Tree Sparrows and nearly 1000 handlings of Slate-colored Juncos. All birds were banded with government bands and colored plastic rings (A. C. Hughes, Hampton Hill, England) to permit individual identification.

We used Japanese mist nets during spring and fall migration when temperatures were above freezing. Only ground traps could be used through the winter. Low (1957) has reviewed the use of mist nets. We caught most of the birds during the winter in Mason traps which were kept continuously baited and free of snow. The feeding areas were cleared at dawn after a snowfall. Traps were left open when not in operation. The differences in weight between birds caught in nets and in traps on the same day are insignificant,* and weights from both sources are treated equivalently.

Every hour, birds were gathered, measured, and weighed to the nearest 0.lg., and their fat was determined by inspection. Classification of fat will be discussed later. Data on each trapping or field identification were entered on the bird's individual card, so that the record of any single bird was available for reference throughout the winter. All birds were released from one site peripheral to the trapping area.

We made regular field observations of the winter flock to determine the size, behavior, composition and changes of the winter population. Most of this work was concentrated in the winter of 1956-57.

Several sources of bias inherent in samples obtained by standard banding procedures should be recognized. For statistical treatment, population samples must be random. Any bander will recognize that non-randomness is introduced into studies of this type. We would like to discuss seven of the causes of bias.

Mist nets give a random sample of low-flying birds. Some birds readily learn to avoid nets, however (Low, 1957; personal observation).

---

*Significance is used in statistics to mean that the probabilty (P) of a given relationship or difference occurring by chance is less than 5 in 100. An event is significant when P=<.05, and insignificant when P=>.05. A relationship or difference is highly significant when P=<.01. See Snedecor (1956) or any standard statistical text for further explanation.

Since we used nets little, and only in fall and spring, we do not believe any error has been introduced.

Some individuals were particularly "trap-shy", especially in the winter population of Slate-colored Juncos; and others, young and sick individuals, may have accounted for too high a proportion. After eliminating obviously sick or injured individuals, however, Tree Sparrow weights from traps did not show any marked skewness (a distortion of the normal curve of frequency distribution) that would indicate such a bias had been introduced.

During migratory periods, both nets and traps capture newly-arrived birds more frequently than earlier arrivals because they are actively flying and seeking food. Samples from both nets and traps taken the afternoon before a migratory flight include few birds. Our field and laboratory observations indicate that this time is largely spent sleeping or resting. This bias applies, however, only to samples directly concerned with migration and does not affect means over longer periods.

"Trap gorging" was rarely found in repeat birds and only occasionally in birds trapped for the first time. By trap gorging we mean the cramming of the bird's crop full of the food used to bait a trap. The crops of birds caught ranged from full to nearly empty, and did not influence the normal distribution of weight means.

Sex and age may be determined with fair certainty before the prenuptial molt in Tree Sparrows (Heydweiller, 1936), and also with nearly complete accuracy in the Slate-colored Junco. Skewness is introduced into junco data (Figures 4c and 4d) by the large proportion of young and female birds. This is not significant, however, and does not require separation of the data or special treatment. Determinations of age and sex are less reliable for Tree Sparrows because the size differences between age groups and sexes are proportionately less than in Juncos (cf. Table II; Baumgartner, 1938). Proportions of young to adult and male to female were constant in both species in trap and net samples throughout the study periods.

Blake (1956) has called attention to the rapid loss of weight in birds held without food. We conducted experiments during the winter of 1956-57 which indicated a negligible weight loss when birds were held in subdued light or in darkness (less than 0.2g.) in the first half-hour after being removed from traps or nets. Although we attempt to process all birds during this period, large single trappings during 1956-57 sometimes required more time to complete processing and these have introduced some error. We feel that no serious error has resulted in our means, however.

Data from new and repeat birds have been treated equally in arriving at means. We feel this is justified by the insignificant difference between weights of new and repeat birds taken on the same day, the high and consistent standard deviation, and the variability of individual weights from hour to hour and day to day.

Jack Hailman, Roger Payne, and members of the Harvard Ornithological Club helped in banding and field observations, and neighbors of the Sanctuary, particularly Mr. and Mrs. Harrie Dadmun have reported color-banded birds. Dr. Ernst Mayr and Mr. Terrell H. Hamilton have made helpful suggestions for the manuscript. Dr.

RESULTS

I. THE WINTER POPULATION

We will discuss the winter population in a later paper, and will discuss here only a few points to the topic of weight, fat, and migration. The "winter flock" is composed of a loose gathering of foraging groups brought together by the availability of food, cover, and suitable habitat as controlled by weather conditions. Foraging groups are loosely integrated groups, usually of four to eight birds, traveling and feeding together for most of the winter. Part of the bond holding these as a group seems to be habitat and habit; part seems to be individual familiarity resulting, perhaps, from previous acquaintance. Mrs. Sabine has discussed winter flocks of Juncos and Tree Sparrows in a series of papers (1949, 1955, 1956). We think that her discussion of integration applies to foraging groups rather than the entire flock.

A.   Slate-colored Junco

Migrant Juncos move through the farm in large numbers in spring and fall, stopping for a period of several days to a few weeks. Migrants were present from the first days of field work in late October 1956. They first appeared on 25 September 1957. They continued to pass through until the end of November both years. On the other hand, winter foraging groups had already established foraging areas by the middle of November. About sixty individuals were present throughout both winters. Spring migrants arrived in numbers (about 200) on the night of 12-13 March 1957, and wintering birds began to move out about the same time both years.

B.   Tree Sparrow

Fall migrant Tree Sparrows seem to prefer river valleys to our upland study area and few birds were seen in the migration period. The first Tree Sparrows in 1956 were found on 24 November 1956, and of nine caught on that date, one remained for 110 days as a member of the winter flock. In 1957-58, a single Tree Sparrow was seen from 3 November with a Junco foraging group, but the species did not arrive in numbers until 31 December. The arrival on winter foraging areas seems to be strongly influenced by weather and the feeding conditions in the river valleys. In 1956-57, early snows and cold weather brought in winter flocks by mid-December, whereas the mild and snowless December of 1957 did not bring birds into the farm until late December and early January. In both years, migration was over by 1 December.

Our winter population numbered about fifty individuals in both winters, but a number of foraging groups from adjacent areas were forced to our feeding areas by the prolonged period of snow cover from

late December to mid-January in 1956-57. Some of these birds remained for the rest of the winter, but many disappeared and we presume they returned to their original areas.

Winter birds left almost en masse from the farm on the night of 14-15 March 1957, leaving only a few members of the flock and some migrants. No marked departures were noticed in 1957-58 but migration seemed to be later; that is, from the third week of March to the second week in April.

Figure 1 shows return and recovery data for individual Tree Sparrows in the winter flock during each of the two years. The reason for the smaller number of records for 1957-58 is that trapping and observation were concentrated on a small area. Ninety-five per cent of the flock was color banded by the middle of January 1957, and about sixty per cent in 1958. These birds provided us with information on foraging groups.

Flock behavior is very similar in Tree Sparrows and Juncos. Juncos confine their foraging more to edge areas and brush than Tree Sparrows. We think that the looser foraging areas, more frequent foraging group contacts, and changes of foraging areas we found in Tree Spar-
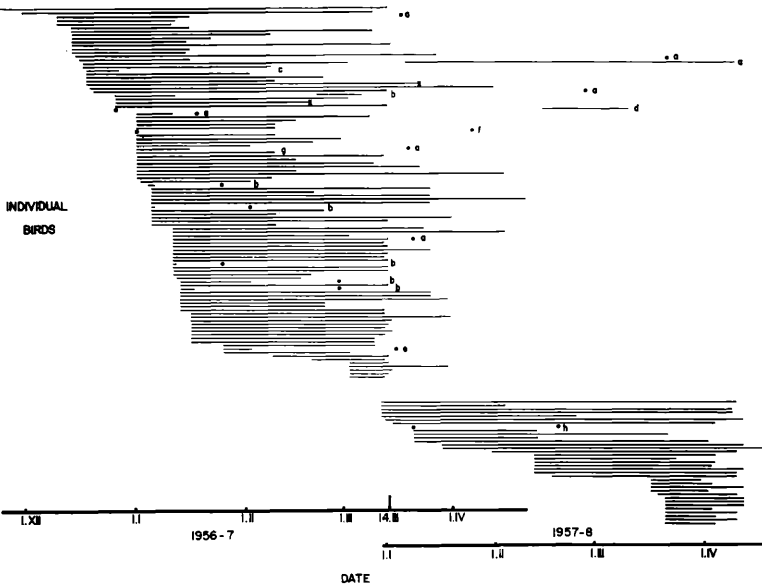

Figure 1. Length of stay of individual Tree Sparrows.

The time between date of banding and the last known record for an individual Tree Sparrow on Drumlin Farm is represented by each line We have included only birds present for thirty days or more except in March. All returns and recoveries through August 1958 are shown, regardless of recorded stay on the farm. The following symbols are used in the graph: circle, a single observation; X, dead; a, return 1957-58; b, repeat ½ mile northwest of banding area; c, recovered Wellesley, Massachusetts; d, recovered Storrs, Connecticut; e, recovered Lincoln, Massachusetts; f, recovered Lexington, Massachusetts; g, recovered Lincoln, Massachusetts (dead); h, recovered Malden, Massachusetts.

Our observations of 14 March 1957 are discussed in the text.

Dates are indicated by arabic numbers preceding Roman numerals which indicate months.
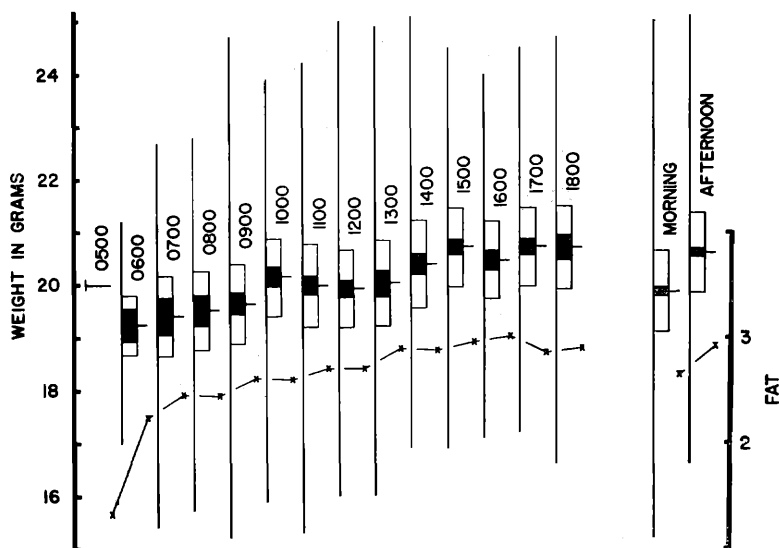
Figure 2.   Diurnal Weight and Fat Increase.
          a. Tree Sparrow (above)
          b. Slate-colored Junco (below)
     Weight data are shown for each hour, and include both winters. The vertical line represents the range of weights; the open rectangle, one standard deviation (1 X S.D.) ; and the solid rectangle, three standard errors (3 X S.E.).   Non-overlap of the solid rectangles indicates that the means (represented by horizontal lines) are significantly different.   After Mayr and Rosen (1956).
     Sample statistics are not graphed when sample sizes are smaller than seven. Mean of fat data for each hour is represented by an X below the weight data.

TABLE I. MEAN WINTER WEIGHTS*

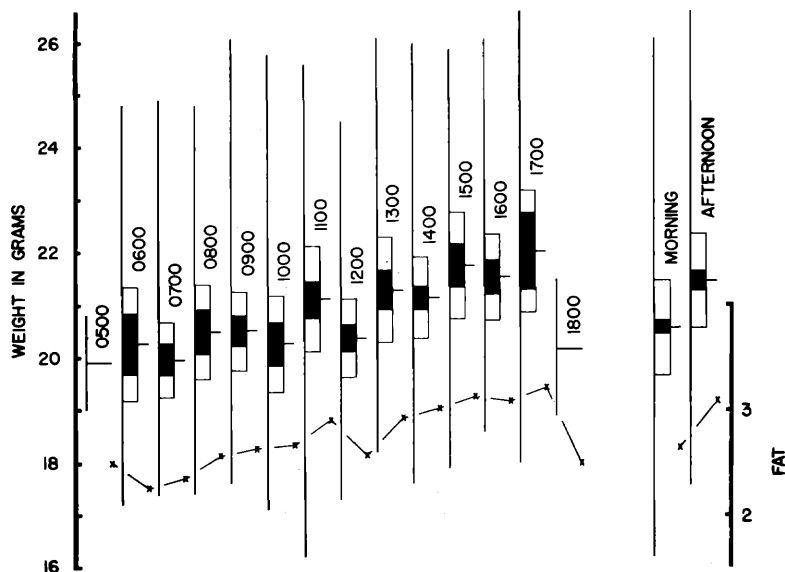|	Sample Size	Mean Weight	S.D.	Minimum-Maximum**	Range	Range Expressed as % of Mean Weight	Fat***
1956-1957							
Tree Sparrow	1198	20.17g.	1.57g.	15.2(14.7)-24.7g.	9.5g.	47	2.76
Junco	181	22.19	1.82	17.7(15.4)-26.0	8.3	37	3.06
1957-58							
Tree Sparrow	447	20.33	1.54	16.4-25.1	8.7	43	2.81
Junco	675	20.88	1.86	16.2-26.6	10.4	50	2.80
1956-58 (All data)							
Tree Sparrow	1645	20.22	1.56	15.2-25.1	9.9	49	2.78
Junco	856	21.16	1.92	16.2-26.6	10.4	50	2.84

*Mean is the arithmetic average, *i.e.*, the total divided by the sample size. Sample standard deviation (S.D.) is a measure of variability in the sample. The mean, plus and minus the standard deviation, includes two-thirds of the data in the sample. Standard Error (S.E.) is a measure of the reliability of the sample. S.D. has been calculated using n-1 (Snedecor, 1956).
**Minima for 1956-57 in parentheses indicate low weights obtained experimentally.
***Fat values represent the mean of all determinations of visible lipid reserves based on a scale of 0-5. (See text).

TABLE II.   COMPARATIVE WEIGHTS OF TREE SPARROWS AND SLATE-COLORED JUNCOS

	Mean Weight	Period of Weights	Sample Size	Maximum Weight	Minimum Weight	Locality	Source
A. Tree Sparrow	18.4g.	winter	12	20.2g.	16.5g.	Ohio	Nice, 1938
	19.05	yearly	—	22.7	15.0	Manitoba	Baumgartner, 1938
	16.90	summer	10	—	—	New York	Heydweiller, 1935
	19.53	winter	472	—	—	Manitoba	Amadon, 1943
	18.53	winter	134	20.50	12.90	Ohio	Stewart, 1937
	19.59	winter	48	22.38	17.40	New England	Wetherbee, 1934
B. Slate-colored Junco	20.2	winter	159	—	—	Ohio	Nice, 1938
	21.25	winter	169	24.9	18.2	New York	Bender, 1949
	21.4 M.	winter	54	—	—		
	19.9 F.		63	—	—		Baldwin and Kendeigh, 1938
	20.0 Ad.		27				
	18.4 Im.		14				
	20.88	winter	171	25.10	14.75	Ohio	Stewart, 1937
	19.5	winter	597	27.6	14.7	Michigan	Becker and Stack, 1944
	20.94	winter	171	26.47	16.0	New England	Wetherbee, 1934

rows is the result of the feeding in more open areas. We do not agree
with Heydweiller (1935) that it is impossible to attribute to these birds
a "uniform group habit", which we assume refers to an integrated
foraging organization—only that this "habit" is more difficult to
analyze.

In a recent paper, Sargent (1959) could find no subgroup affiliations
among Tree Sparrows and supported Heydweiller's conclusions (1935:
above). However, trapping techniques are relatively insensitive for
verifying foraging group associations.

From long periods of observation and simultaneous observations at
several points along foraging routes, we found that foraging groups
rarely remain at one area for longer than 20 minutes, and more usually
only about 10 minutes regardless of abundance of food. Except during
one or two prolonged periods of heavy snow cover, the chances of trap-
ping even two or three members of a foraging group together are small,
and chances of repeated capture of the same individuals together much
less, so Sargent's results are not unexpected.

While flock structure is relatively unstable and influenced greatly by
snow cover, foraging groups of Tree Sparrows seem to have roughly
the stability of Sabine's flocks (1956). Individual association, however,
is revealed only by extensive field observation of individually color-
banded birds.

II. WINTER WEIGHT AND FAT

A. MEAN WINTER WEIGHT

We have become convinced that mean weights for a species are
meaningless without interpretation. They are useful only in descrip-
tive work to provide a norm for statistical comparisons.

The means for Juncos and Tree Sparrows calculated during this
study, and based on all repeat, return, and new weights, are given in
Table I. They include only data taken at Drumlin Farm.

Mean Tree Sparrow weights in our study are higher than other
weights reported in the literature in all cases (*cf.* Table II), because
our sample includes many weights at or near the winter weight peak.
Feeding intensity was directly proportional to snow cover and inversely

TABLE III. DIURNAL WEIGHT CHANGES

	Minimum Mean	Maximum Mean	Differ- ence (Range)	Range Expressed as % of Mean Winter Weight
Tree Sparrow				
1956-57, Hourly Means	18.95g.	20.77g.	1.82g.	9.0%
1957-58, Hourly Means	19.24	21.24	2.00	9.8
1956-58, Morning- Afternoon Means	19.87	20.60	0.73	3.6
All hourly data, both winters	19.24	20.71	1.47	7.3
Slate-colored Junco				
1956-57, Hourly Means	21.12	23.45	2.33	10.5
1957-58, Hourly Means	19.96	22.03	2.07	10.0
1956-58, Morning- Afternoon Means	20.74	21.87	1.13	5.3
All hourly data, both winters	19.96	22.34	2.38	11.2

proportional to temperature. Feeding intensity determined frequency of trapping so that most of our weights are from periods of cold weather; *i.e.*, when weights are highest.

The difference between mean Tree Sparrow weights in the two winters of this study are not significant, and means of the fat classes between the two winters are in agreement.

Mean Junco weights from 1957-58, which contained many weights of fall and spring migrants, agree with published means. Our 1956-57 mean reflects the winter peak. The fat mean is also higher.

Juncos have a higher standard deviation which suggests probably the result of a greater age and sex weight variation. We suggest that the standard deviations (S.D.) of Tree Sparrows and Juncos as found in this paper, 1.6g. and 1.9g. respectively, approach the population standard deviation (σ).

B. DIURNAL VARIATION

1. *Diurnal Variation in Weight*

Daytime weight variation in Tree Sparrows and Slate-colored Juncos is shown graphically in Figure 2. Mean weights per hour were calculated using all birds trapped during that hour. All times are Eastern Standard Time.

The two species show a similar pattern. Tree Sparrows have a morning peak around 1000 and Juncos around 1100. Tree Sparrows have an afternoon weight peak at 1500 (shown more clearly in 1957-58

TABLE IV. VISIBLE FAT

Fat Class	Furculum*	Abdomen	Remarks
0	None or trace; the region is concave.	None	Found only in moulting and sick Juncos and Tree Sparrows.
1	Fat present, but the region is deeply concave; clavicles visible.	Trace	Seldom found in winter.
2	Filling, but the region is still concave; some covering of clavicles.	Not covering; some between intestinal folds and/or in small patches.	Intermediate condition frequent in Tree Sparrows.
3	Filled, clavicles covered; some overflowing furculum, but still concave.	Covering pad, but not markedly mounded.	
4	Filled, furcular fat nearly level with pectoralis muscle, overflowing up interclavicles and over *anterior* pectoral muscles.	Mounded pad, becoming distended.	
5	Convex pad, overflowing the length of the furculum, but never extending over ventral pectoral muscles.	Greatly distended mound.	Usual only during migration; very rarely found in Tree Sparrows.

*The furcular or interclavicular region is the depression formed between the attachments of the pectoralis muscles to the furculum or "wish-bone," and the coracoids, forming a V running toward the spinal cord and the pectoral girdle, through which the neck protrudes.

data) while Juncos tend to have the peak at sunset. For comparative
purposes, morning averages include sunrise to 1400 weights, and
afternoon averages 1400 to sunset weights.

Diurnal weight variation is summarized in Table III.

Nice (1937) found a 4.3-4.9% daytime weight increase in Song
Sparrows *(Melospiza melodia)*. In 1938 she listed diurnal weight
increases by per cent for several species. These ranged from 3.5% for
the House Finch *(Carpodacus mexicanus)* to 10.8% for Slate-colored
Juncos, and Owen (1954) lists variations up to 15%. The ranges given
by our hourly means correspond to those for other small passerines.

A close approximation of diurnal variation may be obtained by
doubling the variation between morning and afternoon means if in-
sufficient hourly data are available to use hourly means.

Diurnal weight increases compensate for nocturnal weight decreases.
Our records during the winter of 1956-57 showed the mean diurnal
weight increase of all Tree Sparrows to be 1.82g. (Table III). During
that winter, a total of 321 birds were held overnight, and weighed
before sunset and again before release after sunrise.* The mean loss
of these birds was 1.88g. The only bird weighed before sunset and
again early the next morning, after spending a night in the wild, was
Tree Sparrow 59-03586 (Figure 6a). She lost 1.9g. from 1700 on the
evening of 9 February 1957 to 0800 on the morning of the tenth. (The
mean temperature was 38° F. on 9 February).

Weight increases during the first two hours in the morning are
probably largely due to food in the crop and gut, although most of our
data were obtained after some feeding had been done. After this, there
is a relatively constant amount of food in the gut. This means that
diurnal weight increase involves stored energy, largely in the form
of subcutaneous fat.

2. Diurnal Variation in Fat

The classification of stored fat which we have used in this study,
given in Table IV, has been modified from McCabe (1943) and Wolf-
son (1954 a,b).

Although some experience is needed to make consistent fat determina-
tions, close agreement of weight and fat observations indicate the
reliability of the method. Mean weights of the four fat classes we
found are significantly different for both species, as shown in Figure 3.
The trend in the differences between the means is reversed in the two
species. In Juncos from Class 1-5, the differences are 0.65g., 1.42g.,
1.27g., and 1.59g., which is a general increase with increasing fat class.
Tree Sparrows, however, from Class 1-4, show differences in means of
1.36g., .96g., and .72g., which is a general decrease with increasing

*Overnight holdings during 1956-57 were planned to compare weight loss of
birds overnight under different temperature conditions. The first three holdings
of birds at environmental temperatures and control groups at room temperature
(20° C.) showed a positive correlation of weight loss with temperature. How-
ever, we had large trappings just before sunset in late January and were forced
to hold all of the birds overnight. The significance of this correlation was lost,
due to delays in weighing of some individuals, either in the evening or morning
hours. We plan to repeat these experiments under controlled conditions with
simultaneous body temperature recordings.

fat class. This suggests some fundamental difference in the relation of fat deposition to body weight in these two species (Helms, 1959).

The mean of the weight difference between all fat classes is 1.23g. for the Junco and 1.01g. for the Tree Sparrow.

In arriving at the means of the fat classes, we rounded to the nearest number (+ and — signs were frequently used in taking the original data) and averaged the whole numbers. This produced error in small samples. Bogus precision should not be read into the graphed fat data. These fat data are based on an artificial scale and should not be interpreted as total lipids, although changes in fat classes do represent changes in lipid reserves. Rather, they provide comparative data with weights. Agreement is usually excellent.

Figure 2 shows that fat changes during the day closely follow weight changes. These changes are summarized in Table V.

We can find no published data on percentage fat increases with which we can compare our results, and the different systems of fat classifications different authors have used would make such comparisons dangerous. The pattern of daytime fat increases in the two species
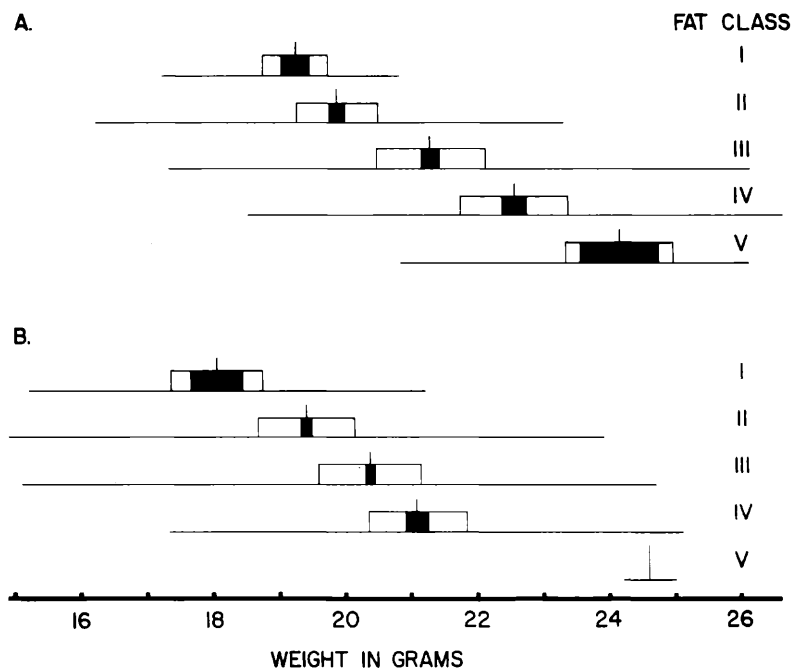

Figure 3.   Mean Weights of Individual Fat Classes.
            A.   Slate-colored Junco
            B.   Tree Sparrow
   All weights are graphed according to fat classes.   Horizontal lines indicate range of weights; the open rectangle, one standard deviation (1 X S.D.); and the solid rectangle, three standard errors (3 X S.E.).   Vertical lines indicate sample means.   After Mayr and Rosen (1956).
   Mean weights in each fat class for both species are significantly different by inspection.   Only two Tree Sparrows in fat class V were seen.

TABLE V.   DIURNAL FAT CHANGES

	Minimum Hourly Means	Maximum Hourly Means	Difference (Range)	Range Expressed as % of Mean Winter Fat
Tree Sparrow				
Hourly Means	2.25	3.15	.90	32.0
Morning-Afternoon Means	2.66	3.05	.39	13.9
Slate-colored Junco				
Hourly Means	2.27	3.17	.90	31.7
Morning-Afternoon Means	2.68	3.12	.44	15.5

is the same. As is the case with weight increases, an approximation of the percentage fat variation may be made by doubling the morning-afternoon percentage increase.

Diurnal fat increases are largely offset by nocturnal losses; for example, during the winter of 1956-57, the mean diurnal fat increase was .66 fat classes during the day, and 214 birds held overnight experimentally lost .33 fat classes. The apparent difference in fat class is probably caused by continued use of stored fat in the course of the early morning after feeding has started and before fat is deposited again. Our observations indicated that fat deposition and utilization usually lagged one to two hours behind weight increase and decrease. Wallgren (1954) found that in the Ortolan *(Emberiza hortulana)* and Yellow Bunting *(Emberiza citrinella)* seed food passed through the gut in two hours and twenty minutes. Kendeigh (1944) reported that about one and one-half to three hours are required for food to be absorbed in the House Sparrow *(Passer domesticus)*. These various approximate measures of the time taken to digest food suggest that fat deposition starts at least one hour after the beginning of feeding. Individual records show this more clearly than averages.

It is interesting to note that Tree Sparrows gained on an average 1.9g. in the course of a day (Table III) while Juncos gained 2.2g. Table V shows that both species gained nearly one fat class—a mean gain of about 1.0g. in Tree Sparrows and 1.2g. in Juncos. Our own data indicates that the amount of food in the alimentary tract may

TABLE VI.   MORNING-AFTERNOON WEIGHT DIFFERENCES

	Tree Sparrow		Slate-colored Junco
	1956-57	1957-58	1957-58
October I	—	—	1.05g.
October II	—	—	0.61
November I	—	—	1.15
November II	—	0.46g.	0.28
December I	—	0.75	0.10
December II	1.20g.	—	0.22
January I	0.64	0.96	0.23
January II	0.87	1.29	1.77
February I	—	—	—
February II	0.50	1.46	1.02
March I	0.58	0.44	0.28
March II	—	0.54	0.39
April I	—	0.15	1.44

contribute about 1.0g. to the body weight of Tree Sparrows during the day. Assuming a similar weight for food in the gut of Juncos, diurnal weight increase in the two species is attributable somewhat more to fat increase than to ingested food material. Fat increases form a higher percentage of the increase in Juncos.

3. *Seasonal Changes in Diurnal Variation*
Table VI gives the differences between morning and afternoon means for those half months in which we have reliable samples.

It would seem that diurnal variation increases in both species toward the mid-winter weight peak. Slate-colored Juncos also show increased diurnal variation during the migratory periods. More data are needed.

4. *Individual Records of Diurnal Variation*
An extreme example as illustration of the variability of fat and of weight change is provided by Tree Sparrow 59-03586 (Figure 6a), who weighed 19.4g. at 1000 on 26 January 1957. She was held four hours without food and water, as part of a weight loss experiment, losing 1.7g. during this period (released at 1400). When captured at 1700, three hours later, she had gained 1.9g., and two fat classes. Even though we assume an empty alimentary tract on release and a full tract on recapture, she added 0.5 to 1.0 grams of fat.

Our experiments during the winter of 1956-57 indicated a weight loss of 1.2g. to 1.5g. during the two to three hours necessary to empty the gut, attaining a post-absorptive condition, and including the normal metabolic use of energy. Weight loss of inactive birds in post-absorptive condition over two to three hours was 0.2g. to 0.3g. This weight loss corresponds to the normal metabolic use of energy. Thus the weight of material in a full gut is 1.0g. to 1.3g. Gut contents which we weighed rarely exceeded this figure unless the crop was completely filled. However, 59-03586 had no seeds in her crop. This would indicate .6g. to .9g. of fat deposition in this bird as a minimum during these three hours. It is interesting to note that her metabolism was "set" to convert food energy to fat as is the usual case during the day in winter, and may be the result of temperature adaptation. Normally, she would have continued to eat in this period. Even though she was unable to eat in this period, she was unable to change the "set" of her metabolism. She must have been a very hungry bird when released!

Junco 25-62007 is an illustration of the use of fat as a source of energy and of toleration to starvation. This bird averaged 21.7g. on three December 1956 trappings, and fat class of 3. On 28 December he weighed 22.0g. at 1700 with a fat class of 3, when placed in a carrying case to be released the next morning. He was held accidentally until 1400 on 30 December, a total of forty-five hours without food and water. When found, he had lost 5.3g. and had a fat class of 1. After receiving special care, he was released on 12 January weighing 17.4g. with a fat class of 2. During six successive captures from then until 16 January, his fat remained 2 and his weight averaged 16.6g., although the weather was cold and the ground snow-covered during this period. He was still in the winter flock on 13 March and in apparent good health. It may be that he recovered his normal body

weight following the severe weather into which he was released, and
that once he recovered, he no longer entered our traps.

5. *Discussion and Summary of Diurnal Variation*

Diurnal weight increases are accompanied by fat increases, and are
matched by losses at night. Food intake and the storage of food as
fat are two main sources of weight increase during the day in winter.
Weight increases most rapidly during periods of most active feeding
in the early morning and afternoon hours, although fat increases
steadily during the daylight hours.

Fat is known to be a ready source of reserve energy in birds,
furnishing twice the energy per gram produced by carbohydrate metab-
olism. It is used to meet the demands of cold nights in maintaining
body temperature and other metabolic functions. These fat reserves
must be important in the emergencies created by storms which may
make food difficult to find.

Seibert's study of food intake (1949) in several species provides
some interesting comparative data for the Junco, and raises several
questions. He found that Juncos used about 18 Calories/bird/day of
metabolizable energy (gross energy or energy contained in the food
consumed minus the energy of undigested food remaining in the excre-
ment) at 28°F. (—2°C), the comparable mean January temperature in
our study area at a ten-hour photoperiod (from graph, p. 136).
Assuming that mean diurnal weight increase in the Junco represents a
net addition of about 1 gm. of fat/bird/day as indicated in this study,
or 9.5 Cal/bird/day, and considering the lowered nocturnal metabolic
rate and longer night in winter, the roughly equivalent energy use
during the day (18 Cal.—9.5 Cal.) conforms to the overnight use of
fat deposited during the day (9.5 Cal.).

Seibert suggests that photoperiod and temperature are the primary
factors limiting the northward distribution of Juncos in winter. Several
difficulties are presented by his extrapolation. (1). Experimental data
were gathered on birds in spring and fall which were not cold-adapted
as indicated by mean body weight (20.1 gm. at —13°C compared with
field means in this study ranging between 22 and 25 gm. in January and
February), even though the experimentals were in energy balance
(energy intake equalled energy outgo and body weight remained con-
stant). (2). Limiting conditions were based on the maximum rate of
energy absorption observed, or what Kendeigh (1944) has called
"potential energy intake." It would seem that this figure may be
much higher than found in experimental conditions and may reflect
the lack of cold-adaptation. Rowan (1929) held Juncos outdoors in
winter in Edmonton, Alberta, several hundred miles north of the
normal winter range. Under natural photoperiod with temperatures
ranging to —52°F., these birds survived much more adverse conditions
than would be possible according to Seibert's data. This supports our
belief that the important limiting factor in northward distribution of
wintering Juncos is food availability *per se,* which is in turn, largely
dependent in buntings on the occurrence of prolonged winter storms
and on mean conditions of snow cover (*cf.* Lack, 1954).

The idea that the entire winter day is used in feeding is implicit in
many studies of energy consumption in birds. A less misleading state-

ment would be that during the colder winter days, little time is spent in activities not associated with feeding. Small birds show feeding rhythms during the day, both in the field and under laboratory conditions. During a normal winter day, foraging individual Tree Sparrows spend a maximum of six to ten minutes in feeding activity (*i.e.*, foraging and feeding), followed either by a period of perching and resting, or social activity which frequently carries the group to another foraging area. An individual's non-feeding periods rarely exceed 20 minutes. Captive Tree Sparrows have non-feeding periods about 12 minutes long in late winter.

Food intake at each feeding period was generally not over 0.2 gm. (based on the weight of the number of millet grains observed to be handled) after the mid-morning period. Feeding was more intense earlier. Under natural conditions where food was not artificially provided, foraging periods would naturally be longer in each feeding cycle, but observations in areas on the farm where birds were foraging naturally indicated that the same rhythm of feeding and non-feeding activity persists. This activity rhythm seems to be basic and would be expected from the nature of digestive processes themselves.

These field observations on feeding agree well with food consumption of captives. Data on Juncos (Seibert, 1949) and Tree Sparrows (Weise, 1956) indicate that captives consume 5-6 gm. of food per day at low temperatures. Assuming that wild individuals feed at an even rate throughout a ten-hour day, feeding every 20 minutes (interval probably less) and consuming 0.2 gm. each period (consumption probably less), total food consumption would be six grams. Differences in caloric value of seed food, the relatively highly concentrated food used in experimental studies, and the shorter winter day could easily be made up during the more intense feeding of early morning.

It is apparent from the field observations that activities of the non-feeding period during the winter vary with season and environment conditions to a much greater extent than those of the feeding period, both in duration and in kind. In warmer weather (average and above average temperatures with little snow cover), the non-feeding period is spent in various social activities, toilet behavior, resting and flight, and during the weeks preceding spring migration, in bathing, song and some sexual activity. During very windy or cold weather, however, much of the non-feeding period is spent in inaction, perching, usually low in rather dense cover. When temperatures are below 0°F., individuals regularly perch low in dense cover with contour feathers fluffed and remain quiet for the entire non-feeding period. These birds often appear to sleep although they do not usually tuck their bills into the scapular feathers during the day. Birds flushed in this condition were very sluggish and we caught two by hand. They became very active one to two minutes after capture, had high weights and showed no signs of illness. It seems likely that this was a period of slight torpidity in which body temperature and metabolic rate were lowered to conserve energy between feeding periods. Thus it is important to note that feeding rhythms persist and more time is actually spent resting than feeding even on the coldest days. This may be relatively independent of food supply even though the bird may have to rely on stored energy
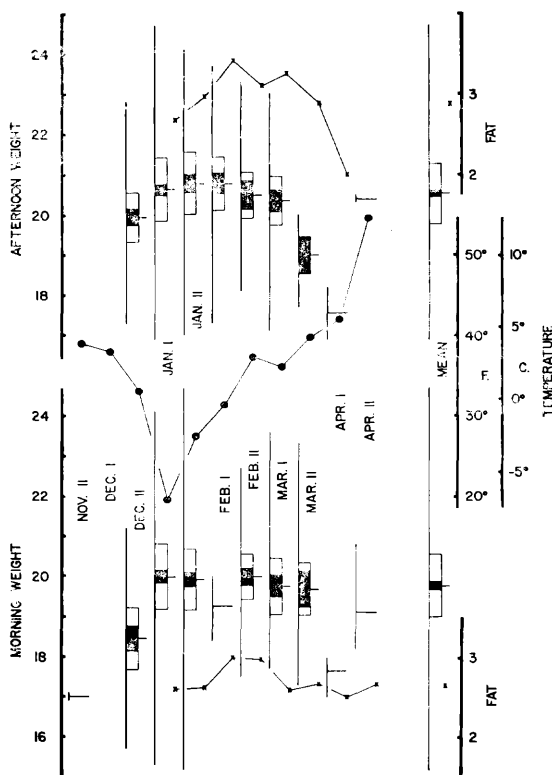
Figure 4a

Figure 4. Morning and Afternoon Weight and Fat by Half-month Means.
  a. Tree Sparrow, 1956-57
  b. Tree Sparrow, 1957-58
  c. Slate-colored Junco, 1956-57
  d. Slate-colored Junco, 1957-58

  Vertical lines represent range of weights; the open rectangles, one standard deviation (1 X S.D.) ; and the solid rectangle, three standard errors (3 X S.E.). Horizontal lines indicate sample means. After Mayr and Rosen (1956). No statistical representations are employed when sample sizes are smaller than seven.
  Fat means are indicated by X, and mean temperature at Logan Airport, Boston, are shown by solid circles. Boston temperatures are graphed for comparison between the two winters, although Drumlin Farm temperatures have been used in all text references.

rather than on food consumption to maintain normal energy metabolism. Although the metabolic needs are determined by temperature and insulation*, food-supply and thus the extent to which a bird has to use stored energy reserves is controlled by snow cover. Survival would be dependent on the duration of heavy cover and the energy reserve of the individual at start of the storm. This supports the idea that snow cover limits distribution, and illustrates the advantage of winter fat deposition in wintering buntings.

*In this consideration, maximum insulation may be regarded as a constant since these birds are cold adapted (*cf.* Scholander *et al.*, 1950).
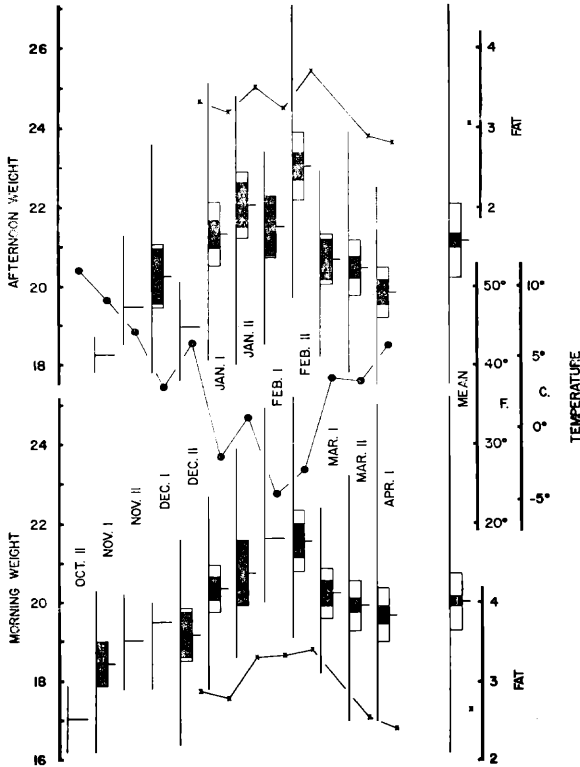
Figure 4b

Low temperatures generally shorten the non-feeding periods, and when food is available, crop contents are greater on cold days. In this way food consumption is increased to meet the increased energy demands imposed by low temperatures whenever possible.

C.   SEASONAL VARIATION IN WEIGHT AND FAT

Figure 4 gives mean weights and fat for Tree Sparrows and Slate-colored Juncos for both winters by half-month means. These include data from Concord, Massachusetts, for 1957-58. Both species reached peak weight and fat between the middle of January and the end of February. After that, weights decreased.

Figure 5 gives morning and afternoon weight and fat by daily means, because half-month mean weights often obscure important day-to-day changes.

Baldwin and Kendeigh (1938) were among the first to seek causes of seasonal variation in bird weights. They found a negative correlation between weight and air temperature for adult Chipping Sparrows
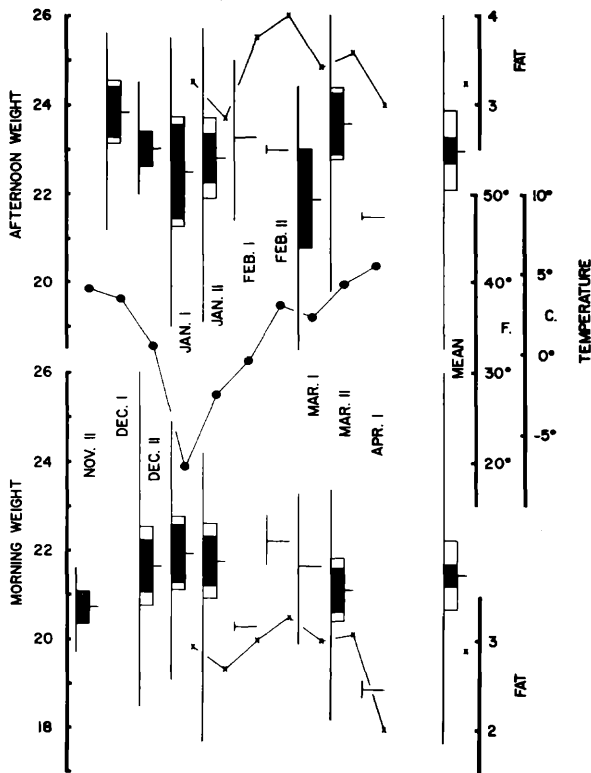
Figure 4c

(Spizella passerina), $(r = -.4)$* and immature Song Sparrows $(r = -.1)$. Negative correlations have been established for several species of small passerines, although correlation coefficients have seldom been reported.

We have analyzed our own data in relation to temperature both by half-month and by daily means. No significant correlation was found between weight and temperature in 1956-57 since we had no temperatures from the study area and were forced to use Logan Airport data (Boston). Correlation coefficients for the second winter of this study are given in Table VII by half months, based on temperature records from South Lincoln.

It can be seen that the correlation of mean weights with mean temperatures is excellent. Morning weights are better correlated than are afternoon weights. This is to be expected because of greater variability in afternoon weights. In all cases, however, better than

---

*Correlation coefficients (r) are a measure of the dependence of one variable on another. r may vary from -1 to 0 to $+1$, an r of -1 signifying perfect inverse correlation, $+1$ perfect direct correlation, and 0 no correlation. Significance has been based on Fisher's table in Snedecor (1956: 174).
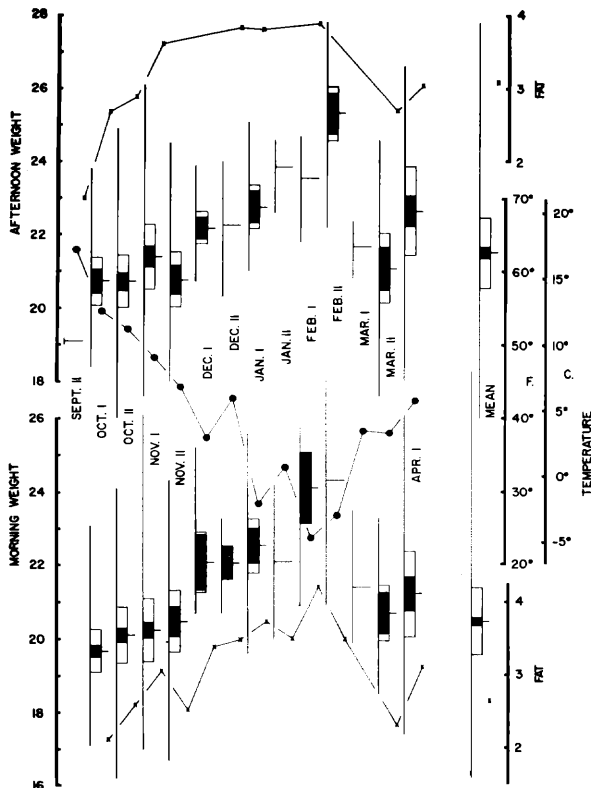
Figure 4d

70% of the mean weight variation can be explained in relation to mean temperature (r^2 X 100 gives the percentage of explained variation).

What is found for mean weights, however, may have no meaning in daily weight fluctuations. Table VIII gives correlation coefficients for both species for all days and for days on which seven or more weights were available. In all cases, the correlation was significant. Thus our data show that half-month mean weights and daily mean weights vary closely in relation to temperature.

Discussion:

In spite of this inverse correlation of weight and temperature during the winter, the control of this relationship and its physiological basis in cold-adaptation are poorly understood.

Unless cold acclimatization in birds is considered a separate phenomenon from cold-adaptation, the mass of data in the literature seems largely contradictory.

The classical view of cold acclimatization has been reviewed by Hensel (Precht, Christophersen and Hensel, 1955; pp. 402-410) in mammals and birds. Acclimatization involves several phenomena in-
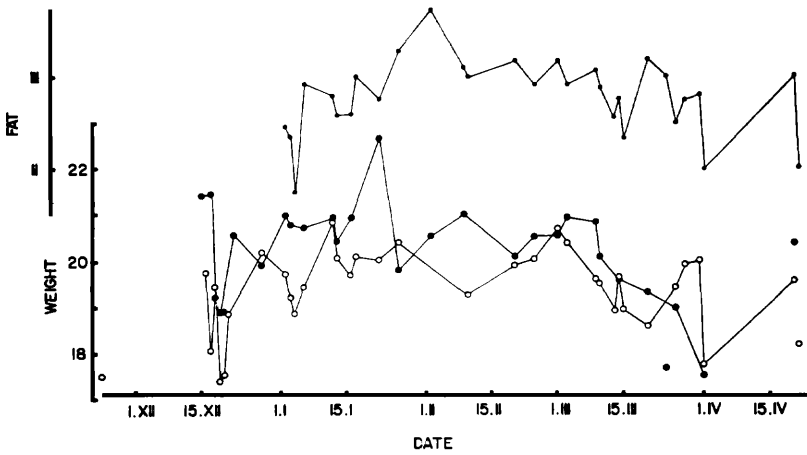
Figure 5.   Morning and Afternoon Weight and Fat by Daily Means.
        a. Tree Sparrow, 1956-57, Weight and Fat
        b. A.   Slate-colored Junco, 1957-58, Weight
           B.   Junco and Tree Sparrow, Fat
        c. Tree Sparrow, 1957-58, Weight

In this graph, morning weights are represented by large open circles, afternoon weights by large black circles; Tree Sparrow fat by small black circles, and Slate-colored Junco fat by small X.   Only means based on two or more weights are connected.
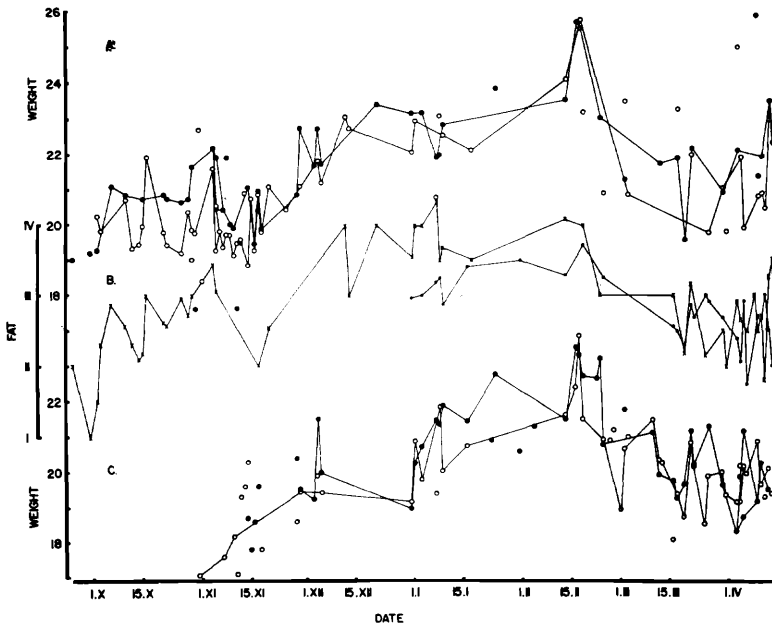
TABLE VII. HALF-MONTH WEIGHT-TEMPERATURE* RELATIONS

	Number of Half-month Periods	Correlation Coefficient	Probability	
Slate-colored Junco				
Morning Means	13	— .9280	< .01	
Afternoon Means	14	— .8462	< .01	Highly significant
Half-month Means	14	— .9145	< .01	
Tree Sparrow				
Morning Means	12	— .9334	< .01	
Afternoon Means	11	— .8667	< .01	Highly significant
Half-month Means	12	— .9205	< .01	

*Half-month mean temperatures are the arithmetic average of all daily mean temperatures, which are in turn the average of the minimum, maximum and midnight temperatures.

cluding the following: increased insulating ability of body cover (fur, feathers); increased fat deposition serving as insulation in aquatic and larger land mammals and as energy reserves in birds and hibernating mammals; changes in melting points of body fat; elevated basal and total metabolisms, a lowering of the zone of thermal neutrality (the temperature range of lowest metabolic rate); increased resistance to cold; and, increased thyroidal activity. Body temperature remains constant during acclimatization.

On the other hand, thyroids of Guinea Pigs activated by cold return to normal after ten weeks in spite of continued exposure to cold, although body weight remains high (Pichotka, 1952). Merkel (1958 b.) found a lowered thyroidal activity in winter in White-throats, *Sylvia communis*, along with a lowered oxygen consumption when compared with summer values, *i.e.*, thyroidal activity and basal metabolism of these cold-adapted birds was lower than that of non-adapted birds. Similar findings with respect to metabolism have been reported in buntings by Wallgren (1954) in *Emberiza* spp., and Schildmacher (1952) in Redstarts, *Phoenicurus phoenicurus*, and lowered winter thyroidal activity in Green Finches, *Chloris chloris* by Schildmacher

TABLE VIII. DAILY WEIGHT-TEMPERATURE RELATIONS

	Number of Days	Correlation Coefficient	Probability	
Slate-colored Junco				
All days	76	— .6071	< .01	
Days with sample size equal to or larger than 7	34	— .7702	< .01	Highly significant
Tree Sparrow				
All days	55	— .6660	< .01	
Days with sample size equal to or larger than 7	32	— .6479	< .01	Highly significant

(1956). Thyroids of White-throated Sparrows which we have autopsied in winter have large follicles containing homogeneous colloid surrounded by a low epithelium, indicating little secretory activity. During both migratory periods, however, White-throated Sparrow thyroids show signs of massive secretory activity (hyperplasia of the epithelium, heterogeneous colloid with numerous resorption vesicles proceeding to glands with almost no colloid).

These results indicate that these animals may pass through a phase of cold acclimatization which coincides with or is superimposed upon fall migration in migratory passerines, to arrive at a physiologically different state of cold-adaptation by the winter period. This adaptation is hastened by low temperatures (Helms, 1960), although many domestic birds and some other passerines, notably the House Sparrow (Miller, 1939), appear to remain in the acclimatization phase (review by Höhn, 1950). Acclimatization and the transition to adaptation, however, is not completely attributable to changes in environmental temperature, since it proceeds under conditions of constant temperature (Helms, 1960). The endogenous nature of the annual cycle is again evident, and to some extent, responsible for this change.

Additional evidence that acclimatization occurs during the fall is furnished by our data that deposition of fat increases towards the end of fall migration, by Kendeigh's data (1934) that resistance to low temperatures as measured by survival time increases, and by various data that metabolism increases (Kendeigh, 1949; Wallgren, 1954; Merkel, 1958 c.). Few data are available, however, on changes in insulation during cold-acclimatization. In general, winter plumage is heavier than summer (*cf.* Wallgren, 1954: pp. 52-58). Our own observations on captive buntings suggest that although the main contour feathers are obtained by the end of the post-nuptial molt, the smaller down feathers in the apteria or unfeathered regions are grown during acclimatization and may represent significant increases in insulation. These down feathers are also sensitive to temperature in that many are lost if temperatures are greatly elevated in winter, and grow in again if temperatures are subsequently lowered. To what extent the increased winter plumage serves to reduce heat loss remains unknown.

Control:

Control of these processes is obscure. The activation of the thyroid by cold and the increase in metabolism which this causes is a fairly rapid response during acclimatization, and serves to offset increased heat loss to the environment by increased heat production. However, many other changes occur as described above, leading eventually to cold-adaptation and a return of the thyroid to normal activity. Hensel (Precht, Christophersen and Hensel, 1955: pp. 402-410) suggests that cold acclimatization may be effected by interactions of the thyroid and adrenal cortex under control of the anterior pituitary. Cold-adaptation may indicate that processes which respond more slowly finally attain control. This picture, however, is complicated by potential interaction of thyroidal and gonadal hormones, (Höhn, 1950; Schildmacher, 1958) also under control of the anterior pituitary. The activity of pancreatic

islet tissue is probably also important. Indications that the transition from cold acclimatization to cold-adaptation in captive buntings coincides with the end of the refractory period, the end of fall nocturnal unrest and migratory behavior, a significant drop in weight and fat, the transition of the thyroid to a storage gland, possibly with the exhaustion of tubular lipids in the testis, the accumulation of ascorbic acid in the adrenal cortex, increased body insulation, and that it may be caused by an abrupt drop in temperature, all serve to indicate the complexity of physiological processes involved (Helms, 1960). Control of cold acclimatization cannot be attributed to any one neuro-hormonal system.

Short-term control of weight adjustment to temperature in cold-adapted birds is probably equally complex. Birds show greater fluctuations in body temperatures than mammals, both during the day (Baldwin and Kendeigh, 1932) and seasonally (Merkel, 1958 c.). Seasonal changes amount to about 2°C. and follow air temperature closely. Inverse correlations with body weight are not significant during the year, but they are striking in the winter phase (Merkel, 1958 c., p. 170). During this phase, birds, as mentioned above, have a lowered thyroidal activity. Since hypothyroidism in mammals causes a drop in metabolism, lowered body temperature, and may induce fat deposition even with lowered food consumption, it might be tempting to seek causal relations between winter temperature dependent weight variations and thyroidal activity. A separation of cause and effect is difficult, however, and it seems that reduced thyroidal activity is more intimately related to adaptation than to day-to-day changes. We find no cytological evidence of short-term thyroidal changes in winter-adapted birds. Brock (1959) has found indications of a partial block in preparatory glycolysis in red blood cells of hibernating hamsters. Although daily changes in body temperature in White-throats do not approach the drop in hibernating mammals, very small changes in rates of reaction in birds which have a high inherent tendency to deposit fat might control fat deposition to an extent in winter. The action of low temperatures on hunger and food consumption is obvious (Seibert, 1949), but the means of action unknown. Other endocrine glands could be involved, and there may be some participation of endogenous components, although this is not as clear as in acclimatization.

Summary:

Cold acclimatization, cold-adaptation, and related weight and fat changes are a part of the annual rhythm in buntings but are poorly understood. During acclimatization, fat slowly accumulates and losses overnight caused by migratory activity are rapidly compensated for. During adaptation, weights reach their yearly maximum in wild populations, and relatively rapid adjustments are made to temperature changes during this period, *i.e.*, weight is temperature dependent. Control of weight adjustments during acclimatization and adaptation is probably different.

Although winter weight adjustments are temperature dependent and relatively rapid, this does not imply a precise day-to-day control. Over-

night weight losses appear to be directly related to temperature (foot-note, p. 14), and diurnal increases inversely related to temperature during winter (Table VI), and the two weight adjustments directly related to each other. Correlation of daily mean weights with tempera-ture verifies this. Our data on captive birds, however. indicate some physiological lag, usually about two to four days.

D. INDIVIDUAL VARIATION IN WEIGHT AND FAT

In order to present two pictures of individual variation in weight and fat, the records of Tree Sparrows 59-03586 and 25-62023 are given in Figures 6a and 6b. The records are for the winter of 1956-57.

59-03586, probably an adult female, was present for ninety-four days. Disregarding experimental holdings (solid lines) of over fifteen hours, a relatively constant variation is seen. The decrease of the winter peak in mid-March in this individual is also shown.

25-62023, probably an immature male, was present for one hundred days. Although the variation shown on any one day falls within the normal range, his weights through the winter differ widely, from a low of 14.9g. on 17 January to a high of 21.2g. on 28 February—a range of 6.3g. His tail was lost on 3 January, and on 13 January his weight was high and the tail already 17mm. in length. It does not seem likely, then, that the tail loss was responsible for the lowest weights on 16-17 January. This low may have been due to the low temperature (—15° F.) of the night before, although the population was at its mid-winter weight peak on this date.

Both of these records also show daily trends in fat and overnight losses of weight during experimental holdings.

E. REPEAT RECORDS OF TREE SPARROWS ON THE SAME DAY

Owen (1954) found that repeat records of individuals on the same day may or may not follow the trend of the mean. Birds caught repeatedly on one day may increase in weight, decrease in weight, or remain the same, although these birds follow the normal diurnal trend of variation when averaged. Tree Sparrow repeats on the same day are presented in Table IX.

Gains in weight by birds which repeated twice from morning to afternoon and those that repeated three times, agree closely with the difference between the means of all morning and afternoon weight data (0.73g.).

III. MIGRATION

A. WEIGHT AND FAT

In 1822, Naumann noted fat deposition associated with migration (Farner, 1955). Zeidlitz (1926) found weight and fat increases in several European species, and Linsdale and Sumner (1934) found migratory weight and fat increases in the Golden-crowned Sparrow *(Zonotrichia coronata)*. Baumgartner (1938) found a weight increase during spring migration in the Tree Sparrow. However, it was not until the works of Wolfson (1942, 1945) and Odum (1949) that these weight and fat increases were clearly shown in North American species in a systematic manner. Odum's paper (1949) on the White-throated Sparrow remains the best field study documentation for weight and fat associated with migration.

Figure 6.   Individual Weight and Fat Variation, 1956-57
        a. Tree Sparrow 59—03586
        b. Tree Sparrow 25—62023

See text. Circles represent weight records, X represents an identification in the field by colored bands. Open circle, fat class O; circle with horizontal line, fat class 1; circle with vertical line, fat class 2; circle half black, fat class 3; circle black, fat class 4. Times of records indicated by first two numbers of the nearest hour; *e.g.*, 17 represents 1700. Records connected with straight lines indicate experimental holdings with the time indicated. The line above the average shown on the right of the graph indicates mean weight without experimental weights, and the line below it indicates a mean including all records. Weight in grams is given on the ordinate, and date along the abscissa.

TABLE IX. TREE SPARROW REPEATS ON THE SAME DAY

	Number of Repeats	Net Gain in Weight of All Repeats
Double Repeats		
Morning-morning	88	0.16g.
Afternoon-afternoon	18	0.35
Morning-afternoon	216	0.66
Triple Repeats	29	0.79
Quadruple Repeats	1	1.80
Quintuple Repeats	1	0.20

Other species showing migratory weight and fat increases are found in the buntings (Weise, 1956; Wolfson, 1954c; etc.). Odum (1958) lists several species of vireo and New World warblers in which high fat deposits have been found in birds killed during migration. Various Old World warblers show migratory fat reserves (Merkel, 1938; 1958b). We have found marked fat reserves during both migratory periods on Myrtle Warblers *(Dendroica coronata)*, Blackpolls *(Dendroica striata)*, and at one migratory period on all other species of warblers examined in numbers, as well as fall migrant thrushes *(Hylocichla* spp.), and a captive Lark Sparrow *(Chondestes grammacus)*. This list is far from complete, but suggests that increased fat and weight during migratory periods is a generality in small passerines which migrate. *Fat deposition during fall and spring is not found in non-migratory species* (Baldwin and Kendeigh, 1938), *or in non-migratory populations of migratory species* (Wolfson, 1945).

The apparent exception to this generality is the Song Sparrow (Nice, 1937; 1946). However, Helms (1959) has shown that Song Sparrow weights and fat were significantly higher before a spring migratory flight than after. Patterns of Song Sparrow and Tree Sparrow weight variation are similar, and it appears that both species do exhibit weight increases associated with migratory flight.

Wolfson (1942, 1945) suggested that this weight and fat was part of the physiological preparation for migration and energy storage for prolonged flights. Farner (1955) suggested that this fat deposition might constitute the migratory stimulus, but this now seems unlikely. We feel that fat deposition is only one of several preparatory reactions of the bird which necessarily precede migratory flight as part of the endogenous cycle. All of these preparatory reactions may be influenced by environmental conditions, and we should not expect them to appear in just the same form and same sequence in all species.

Turning to our own data for Tree Sparrows and Juncos (Figure 4 by half-month means, Figure 5 by daily means), we found only a suggestion of weight increase in the last half of April in 1956-57 in our small sample of Tree Sparrows. In 1957-58, in both spring and fall, there was no increase that could be significantly dissociated from normal weight variation. Slate-colored Juncos do show a significant increase in mean afternoon weights and fat, however, in the first half of April 1958. This rise also appears in mean daily weights although peak weights are still under the winter mean weight for the species. There is a suggestion of fall weight increases associated with migration in both species in 1957-58, but this is not statistically reliable.

TABLE X. DAILY WEIGHT-TEMPERATURE RELATIONS DURING
WINTER AND MIGRATION

	Number of Days	Correlation Coefficient	Probability	
Tree Sparrow				
All data				
Fall Migration	16	— .2404	> .05	Not significant
Winter	24	— .5557	< .01	Highly significant
Spring Migration	15	— .0678	> .05	Not significant
Samples equal to or larger than 7				
Fall Migration	2	(Insufficient data)		
Winter	18	— .5692	⌐ .05	Probably significant
Spring Migration	12	+ .1269	> .05	Not significant
Slate-colored Junco				
All data				
Fall Migration	29	+ .2614	> .05	Not significant
Winter	30	— .7361	< .01	Highly significant
Spring Migration	17	— .1817	> .05	Not significant
Samples equal to or larger than 7				
Fall Migration	19	+ .3032	> .05	Not significant
Winter	11	— .9139	< .01	Highly significant
Spring Migration	4	— .8707	> .05	Not significant

The main difficulty we encountered in obtaining data in support of migratory weight and fat increases, *i.e.*, the attainment of a migratory condition in field populations, was one of sampling. Birds are relatively easy to catch in numbers during migratory periods, and during periods of snow cover in winter. However, residents between the end of fall migration and the beginning of winter snow, and following the end of snow cover to spring migration, are hard to trap. It is usually too cold to use nets. Because both peaks, if present, are lower than the winter peak, data from these periods are necessary, particularly in fall, to verify the migratory condition of birds during migration. The fact that we are seldom visited by migrant Tree Sparrows in the study area further complicates interpretation of data in this species.

Laboratory records of individual birds (Wolfson, 1954b,c; Weise, 1956; and others) using weight and fat, show migratory increases more clearly than our field studies. In laboratory studies, the constant availability of food, the elimination of some of the thermoregulation stress, the separation of individuals, and confinement preventing much flying may influence weight and fat changes. On the other hand, migratory samples from the field tend to be biased toward non-migratory birds or freshly arrived migrants.

Because weight and fat increases were not clear for any migratory season in Tree Sparrows, and for fall in Slate-colored Juncos, from our data, we wanted to determine to what extent mean weights during migratory periods were dependent on mean temperature. Correlation data from Table VIII is broken down into winter and migratory periods in Table X.

The correlation of weight and temperature during the winter is good; *i.e.*, weight is "temperature-dependent" during the winter. However, there is no correlation during migratory periods, and this is "temperature-independent" variation.

We do not know to what extent this change between temperature-independent variation and temperature-dependent variation is present in resident populations *(cf.* Kendeigh, 1949).

Discussion:

This change to temperature independence during migratory periods is further indication of a change in control of variation with the phase of the annual cycle as discussed in the previous section. The winter bird seems to be operating at a different physiological "level" than the migratory bird. This "level" can be affected by many environmental factors, but its control is not known.

The change in weight-temperature relations during migration does not seem to be passive and due to change in food supply, since new food is becoming available, including seeds in the fall and the uncovering of seeds and emergence of insects in the spring. Seasonal changes in food type in Tree Sparrows are indicated (Baumgartner, 1937), however, and could influence metabolism. High summer temperatures and the shift to protein diets are probably related to summer low weights, but would not be important at onset of spring migration.

Davis (1955) suggested that spring weight increases might be due to physiological lags in adjusting food consumption to elevated temperatures. We find no evidence in support of this hypothesis. Weight changes in captive birds prior to migration in spring indicate complex endocrine control largely independent of the environment (Helms, 1960). We agree with Merkel (1958 a, c.) that the only source of this weight and fat increase indicated is in increased food consumption.

Control:

Rowan (1925) equated migration with gonadal development in spring, and autumnal regression, emphasizing that migration was only a part of the reproductive cycle. In spite of contradictory evidence, it now seems to us that Rowan may have been more correct than suspected. Schildmacher and Steubing (1952) have reported fat deposition following testosterone injections. Wagner (1956) gives experimental evidence in support of his working hypothesis that ". . . im Winterquartier bereits beginnende Abgabe von Geschlechts-hormonen eine Verstärkung des Zugimpulses und damit die Ausschaltung von Umweltreizen herbeiführt." (pp. 358-359). The resident and migratory status of many British birds is reflected in differences in the gonadal cycle (Bullough, 1943). Our data on captive White-throated Sparrows indicate that androgen and estrogen can cause weight and fat increases within limits in spring. This action can be reversed by progesterone. These actions are reversed in the fall, progesterone stimulating and androgens and estrogens inhibiting weight and fat increases. These actions agree with the normal testicular cycle *(cf.* Marshall, 1951). During the spring, the interstitial cells of the testis are secreting androgen. Marshall (personal communication) has recently discovered that the cholesterol positive tubular lipids, characteristic of the testicular reorganization following post-nuptial collapse, have a progestational activity. These lipids disappear gradually during the fall.

Conspicuous changes in thyroidal activity are also found during migratory periods and have been discussed in relation to cold adapta-

tion. Current experiments (Helms, 1960) indicate a synergistic action of thyroxine and sex steroids on migratory condition in spring. Merkel (1958 b.) found a change in migratory behavior in response to insulin which seems separable from normal hypoglycemia. This suggests that pancreatic islet tissue is also involved, and other endocrines should also be considered.

Summary:

Control of migratory weight variation is largely endogenous and seems to be very complex. It is suggested that at least the gonads and thyroid play roles during these periods. Various environmental influences capable of modifying the timing of migration and the annual cycle in general have been reviewed by Burger (1949), Marshall (1949), and Aschoff (1958). Whatever the bases of seasonal changes in fat deposition may be, their control during migratory periods must be physiologically different than during winter.

B. WEATHER AND MIGRATION, 1956-57

Spring migration had started in the Slate-colored Junco by 1 March 1957, and there was a large flight on 12-13 March. There was no big Tree Sparrow immigration or emigration until the night of 14-15 March. We will review briefly the flock behavior and changes leading up to this period.

On 17 February, we first noted that groups of Tree Sparrows dispersed from their winter foraging areas to other parts of the farm. Juncos became much more conspicuous along their winter foraging routes, and occasionally left them. We noticed increased aggressiveness at feeding areas, and the individual distances (distance to which a neighbor might approach [Conder, 1949]) increased. Dominance and peck order became evident, head-forward threat and chases become frequent. Individuals became more active within groups and groups dispersed and foraged farther. The Tree Sparrow "warble" was heard frequently and Juncos started to sing. Tree Sparrows began singing a week later. On the night of 12-13 March, 200 Juncos arrived at the farm, and occupied areas different from the normal winter birds; by late morning residents and migrants were mixing regularly, although most winter foraging groups remained intact. This, and successive influxes of unbanded Juncos prevented accurate dating of arrivals and departures. The last Junco was seen in the last week of April.

Singing Fox Sparrows *(Passerella iliaca)* arrived; on 13 and 14 March, Cowbirds *(Molothus ater)*, Robins *(Turdus migratorius)*, Grackles *(Quiscalus quiscula)*, and Red-wings *(Agelaius phoeniceus)*, were seen migrating over the farm.

On 13 and 14 March, Tree Sparrows were in full song, feeding actively and moving frequently. Chases, threat, flight, were frequent. There were no noticeable differences in behavior on 14 March from the activity of the previous week, but birds did seem to disappear from the feeding areas earlier than usual. A search of the farm failed to reveal the birds at any of their known foraging areas. As we were coming in at dusk, about 1800, Drury heard a Tree Sparrow flock contact call, a "tsenk," overhead, and watched 30-50 birds fly north

TABLE XI.   LAST RECORDS OF TREE SPARROWS,
14-15 MARCH 1957 FLIGHT

A.   Visual Records of Banded Birds
        13 March — 5 birds last seen
        14 March — 6 birds last seen

B.   Trap Records

| | Prior to Departure | | | Total Season Records | |
| | | | | Mean | Number of Repeats |
Bird	Weight	Fat	Time	Weight	Prior to Last Record
13 March					
686	18.9g.	3	morning	19.6g.	3
658	17.8	2	morning	19.1	12
648	20.3	3	morning	21.0	10
591	19.6	2	morning	20.8	10
589	18.9	2	morning	19.6	14 (also seen 14 March)
14 March					
693	{ 18.3	3	afternoon		
	{ 18.6	4	late afternoon	18.6	3
688	20.3	3	afternoon	20.8	4
613	21.7	3	afternoon	22.7	8
597	17.7	2	afternoon	18.9	16
593	17.9	2	early morning	18.8	15
764	{ 21.4	3	early morning		
	{ 21.2	4	afternoon	20.8	6
719	20.5	2	afternoon	20.8	11
013	21.2	2	afternoon	21.2	4

singly. Although individuals may well have been in sound contact, this flight was different from the normal roosting flights observed previously—in flock structure, amount of calling, and direction. Most of our winter flock of Tree Sparrows left in this flight.

Figure 1 shows that on 13 and 14 March, 24 birds disappeared that had been with us a long time. Both days are considered together, because on any one day we could expect to catch or see half or less of the population. Our field estimate of 60 birds on the 14th with no unbanded birds precluded departure on the 13th, and intensive field work on the 15th failed to reveal more than 10-20 Tree Sparrows. Of these less than half were banded.

Table XI presents the last records of these birds.

Means of weights taken 13 and 14 March of the birds that disappeared on the night of 14 March 1957 are not significantly different from weights of other Tree Sparrows trapped on the same days. Although weights of "migrants" on the 14th were higher than those of birds trapped on the 15th, these differences are not significant $(P = .4 —.2)$. Fat of all birds on the 14th was nearly one half-class higher than on the 15th, although this could be attributed to small sample size and normal variation. Thus, the migrant birds show no conclusive differences from the remaining resident population or from the half-month means.

On 13 March, no birds were heavier than their own mean weight, although on the 14th, two birds equalled their own average or exceeded it. Helms (1959) suggested from data on coastal migrants that

there is preparation for migratory flight in Tree Sparrows which in-
cludes weight and fat increases. The difficulties in detecting these
differences may be attributed to the small size of the increase and to
the statistical problems in inadequate samples. Weight and fat increases
in Tree Sparrows may occur only several days, or even only on the day
preceding, actual migratory flight.

It is also possible that these increases become evident only after
migration is underway. Data on captive White-throated Sparrows
(Helms, 1960) indicate that weight increase begins prior to the first
night of "migration," but amounts to only about half of the maximal
migratory weight attained after migration begins in spring. Since
Tree and Song Sparrow variation is fundamentally different (Helms,
1959), pre-migratory increases may not be found in field studies.

Temperatures on the farm leading up to this flight are: 11 March,
23-49° F; 12 March, 32-42° F; 13 March, 26-54.5° F; 14 March,
38-52° F; and 15 March, 36-47° F. Temperatures were in the 50's
on both the 13th and 14th of March, and may have stimulated the
Tree Sparrows to leave on the second evening. Various authors have
shown the correlation of migratory activity in spring with warm
temperatures (Nice, 1937; Farner, *et. al.*, 1954), although increased
photoperiod seems to be the main timing stimulus for migratory be-
havior (Farner, 1955; Farner and Wilson, 1957).

The weather picture at the time of departure was not "favorable"
for nocturnal migration (Bagg, *et. al.*, 1950; Raynor, 1956). The day
had been sunny but a light overcast (Altostratus) formed at dusk and
remained past midnight. Surface winds were southeasterly 5-8 miles
per hour at sunset, and east-southeasterly 9-14 miles per hour at mid-
night. Stratus clouds were present around 1000 feet and there was
some fog early in the night. A stationary front extended from Syracuse,
New York, across Providence, Rhode Island, and out over the Atlantic,
and had moved but little from the previous day.

C. DISCUSSION

Fat and weight during winter resident and migratory phases of the
annual cycle followed the pattern found in White-throated Sparrows
(Odum, 1949). Laboratory and field results on migratory condition
agree.

Our data on Tree Sparrows, however, resemble Nice's (1937, 1946)
for Song Sparrows. Helms (1959) showed that weight and fat taken
the day before a migratory flight are significantly higher than weights
of arriving migrants, although Song Sparrows may not show a signifi-
cant weight and fat peak during spring migration. A small sample of
Tree Sparrows' weights were not significantly different from one an-
other before and after a migratory flight, but birds taken before migra-
tion were significantly heavier than the mean half-month Tree Sparrow
weight for this period. Song and Tree Sparrow data in these samples
are so similar that they suggest that the two species do show a pre-
flight preparation in weight and fat. We would be very interested to
learn whether more evident changes in weight and fat are found after
the birds are actually migrating. Thus, weights taken further north will
be of especial interest.

SUMMARY

1. Migratory periodicity as a part of the annual cycle in passerines involves actions of various environmental "time-givers" on the internal rhythm of the bird, and the resulting interactions leading to a migratory condition in individual migratory birds. The migratory condition, which involves various physiological changes, including fat deposition, may be studied in the field. Migratory behavior, on the other hand, is more suitably studied under laboratory conditions.

2. During the winters of 1956-57 and 1957-58, weight and fat determinations were made on 477 Tree Sparrows, *Spizella arborea* (over 2000 records), and 572 Slate-colored Juncos, *Junco hyemalis* (nearly 1000 records). The stable winter populations of both winters were about 60 Juncos and 50 Tree Sparrows. These were color banded and followed during the winter and through spring migration. The units were groups of 4-8 birds which usually traveled together for the whole winter.

3. Mean winter weights of Tree Sparrows both winters was 20.22g., S.D. 1.56g., and of Slate-colored Juncos 21.16g., S.D. 1.92g. Diurnal weight variation in Tree Sparrows was 7.3-9.8%, and in Juncos 9.9-11.2%. Daytime weight and fat increases were balanced by overnight loss. About one-half of this daily variation is attributable to fat, and the other half to ingested food. Diurnal variation is greater during mid-winter in both species.

4. A modified scheme for classification of fat based on amounts visible under the skin is given. Tree Sparrows and Slate-colored Juncos have different relations of mean weight to fat class.

5. Birds of both species gain weight in mid-winter from a fall low, and lose weight after mid-winter. Winter weight changes are temperature dependent ($r = -.9$).

6. Data on individual birds and repeat data from many birds are used to validate the mean results.

7. Weight and fat variation becomes temperature independent during migratory periods in both species. Although only the Junco shows a significant migratory weight peak in spring, the temperature independence of weight during migratory periods in both species suggests that different physiological controls associated with migration become operative at migratory periods. These controls remain unknown.

8. The sequence of events in the spring migration in 1956-57 is given. Twenty-four members of the winter population are known to have left on the night of 14-15 March 1957. They were seen to fly north. Weights of departing Tree Sparrows were not significantly higher than those of birds which remained. Other data suggest that Tree Sparrows do have a pre-migratory weight and fat increase.

REFERENCES

AMADON, D. 1943. Bird weights and egg weights. *Auk* **60**: 221-234.

ASCHOFF, J. 1955. Jahresperiodik der Fortpflanzung bei Warmblütern. *Studium Generale* **8**: 742-776.

——————. 1958. Tierische Periodik unter dem Einfluss von Zeitgebern. *Zeits. Tierpsychol.* **15**: 1-30.

BAGG, A. M., W. H. GUNN, D. S. MILLER, J. T. NICHOLS, W. SMITH and F. P. WOLFARTH. 1950. Barometric pressure-patterns and spring bird migration. *Wilson Bull.* **62**: 5-19.

BALDWIN, S. P., and S. C. KENDEIGH. 1932. Physiology of the temperature of birds. Sci. Publ. Cleveland Mus. Nat. Hist. **3**: 1-196.
———. 1938. Variations in the weight of birds. *Auk* **55**: 416-467.
BAUMGARTNER, A. M. 1937. Food and feeding habits of the Tree Sparrow (Spizella). *Wilson Bull.* **49**: 65-80.
———. 1938. Seasonal Variations in the Tree Sparrow. *Auk* **55**: 603-613.
BECKER, G. B. and J. W. STACK. 1944. Weights and temperatures of some Michigan Birds. *Bird-Banding* **15**: 45-68.
BENDER, R. O. 1949. Notes on the Slate-colored Junco. *Bird-Banding* **20**: 180-182.
BENOIT, J. 1950. Reproduction-caractères sexuels et hormones-déterminisme du cycle sexuel saisonnier. Traite de Zoologie, ed. P. P. Grassé, Masson et Cie, Paris, **15**: 384-478.
———, I. Assenmacher, and E. Brard. 1955. Évolution Testiculaire du Canard domestique mainténuà l'obscurité totale pendant une longue durée. *C. R. Acad. Sc.* **241**: 251-253.
—, —, —, 1956. Étude de l'évolution testiculaire du Canard domestique soumis très jeune á un éclairement artificiel permanent pendant deux ans. *C. R. Acad. Sc.* **242**: 3113-3115.
BISSONNETTE, T. H. 1937. Photoperiodicity in birds. *Wilson Bull.* **49**: 241-270.
BLAKE, C. H. 1956. Weight changes in birds. *Bird-Banding* **27**: 16-22.
BLANCHARD, B. D. 1941. The White-crowned Sparrows *(Zonotrichia leucophrys)* of the Pacific seaboard: Environment and annual cycle. *Univ. Calif. Publ. Zool.* **46**: 1-178.
BROCK, M. A. 1959. Unpublished data on hibernation in hamsters.
BULLOUGH, W. S. 1943. Autumnal sexual behaviour and the resident habit of many British birds. *Nature* **151**: 531.
BÜNNING, E. 1958. Die Physiologische Uhr. Springer-Verlag, Berlin. 105 pp.
BURGER, J. W. 1949. A review of experimental investigations on seasonal reproduction in birds. *Wilson Bull.* **61**: 211-230.
CHAPIN, J. P. 1954. The calendar of Wideawake Fair. *Auk* **71**: 1-15.
CONDER, P. J. 1949. Individual Distance. *Ibis* **91**: 649-655.
DAVIS, E. A., JR. 1955. Seasonal changes in the energy balance of the English Sparrow. *Auk* **72**: 385-411.
FARNER, D. S. 1955. The annual stimulus for migration; experimental and physiologic aspects. Recent Studies Avian Biol., ed. A. Wolfson, U. of Ill. Press, 198-237.
———, L. R. Mewaldt, and J. R. King. 1954. The diurnal activity patterns of caged migratory White-crowned Sparrows in late winter and spring. *J. Comp. & Physiol. Psych.* **47**: 148-153.
———, and A. C. WILSON. 1957. A quantitative examination of testicular growth in the White-crowned Sparrow. *Biol. Bull.* **113**: 254-267.
FISHER, H. I., and L. M. BARTLETT. 1957. Diurnal cycles in liver weights in birds. *Condor* **59**: 364-372.
HAFTORN, S. 1951. En undersøkelse over vekt-variasjoner i vinterhalvåret hos kjøttmeis. Saertrykkav Fauna, *Norsk Zool. Foren. Tidskk.* **2**: 83-91.
HAGEN, Y. 1942. Totalgewichts-Studien bei norwegischen Vogelarten. Unter besonderer Berücksichtigung der biologishen Verhaltnisse bei Raubvögeln, Eulen und Waldhühnern. Archiv. für Naturgeschichte, *Zeits. Syst. Zool.* N. F. **11**: 1-173.
HEINROTH, O. 1922. Die Beziehungen zwischen Vogelgewicht, Eigewicht, Gelegegewicht und Brutdauer. *J. Orn.* **70**: 172-285.
HELMS, C. W. 1959. Song and Tree Sparrow weight and fat before and after a night of migration. *Wilson Bull.* **71**: in press.
———. 1960. Thesis in preparation.
HEYDWEILLER, A. M. 1935. A comparison of winter and summer territories and seasonal variations of the Tree Sparrow *(Spizella arborea)*. *Bird-Banding* **6**: 1-11.
———. 1936. Sex, age and individual variation of winter Tree Sparrows. *Bird-Banding* **7**: 61-68.
HÖHN, E. O. 1950. Physiology of the thyroid gland in birds; a review. *Ibis* **92**: 464-473.

KENDEIGH, S. C. 1934. The role of environment in the life of birds. *Ecol. Monog.* **4**: 299-417.

————. 1944. Effects of air temperature on the rate of energy metabolism in the English Sparrow. *J. Exp. Zool.* **96**: 1-16.

————. 1949. Effects of temperature and season on energy resources of the English Sparrow. *Auk* **66**: 113-127.

KLUIJVER, H. N. 1952. Notes on body weight and time of breeding in the Great Tit, *Parus m. major* L. *Ardea* **40**: 123-141.

LACK, D. 1954. The natural regulation of animal numbers. Oxford, London, 343 pp.

LAWRENCE, L. D. 1958. On regional movements and body weight of Black-capped Chickadees in winter. *Auk* **75**; 415-443.

LINCOLN, F. C. 1952. Migration of Birds. Doubleday, N. Y. 102 pp.

LINSDALE, J. M., and E. L. SUMNER. 1934. Winter weights of Golden-crowned and Fox Sparrows, *Condor* **36**: 107-112.

LOW, S. H. 1957. Banding with mist nets. *Bird-Banding* **28**: 115-128.

MARSHALL, A. J. 1949. Weather factors and spermatogenesis in birds. *Proc. Zool. Soc. London* **119**: 711-716.

————. 1951. The refractory period of testis rhythm in birds and its possible bearing on breeding and migration. *Wilson Bull.* **63**: 238-261.

————. 1958. The role of the internal rhythm of reproduction in the timing of avian breeding seasons, including migration. XII Congr. Int. Orn., Helsinki, Abstr.: 18.

————. 1959. Personal communication.

MAYR, E., and J. GREENWAY. 1956. Sequence of passerine families (Aves). *Breviora* **58**: 1-11.

————, and C. B. ROSEN. 1956. Geographic variation and hybridization in populations of Bahama snails *(Cerion)*. *Am. Mus. Novitates* **1806**: 1-48.

McCABE, T. T. 1943. An aspect of the collector's technique. *Auk* **60**: 550-558.

MERKEL, F. W. 1938. Zur Physiologie der Zugunruhe bei Vögeln. *Ber. Ver. Schles. Ornithol.* **23**: (Sonderheft) : 72 pp.

————. 1958a. Zur Physiologie der Zugunruhe nächtlich ziehender Kleinvögel. XII Congr. Int. Orn., Helsinki, Abstr.: 19. (Further data given in personal communication).

————. 1958b. Untersuchungen zur künstlichen Beeinflussung der Aktivität gekäfigter Zugvögel. *Vogelwarte* **19**: 173-185.

————. 1958c. Untersuchungen über Tages—und Jahresperiodische Änderungen im Energiehaushalt gekäfigter Zugvögel. *Zeits. vergl. Physiol.* **41**: 154-178.

MILLER, A. H. 1955. Breeding cycles in a constant equatorial environment in Columbia, South America. Acta XI Congr. Int. Orn., Basel, 1954. *Experientia Suppl.* **3**: 495-503.

MILLER, D. S. 1939. A study in the physiology of the sparrow thyroid. *J. Exp. Zool.* **80**: 259-286.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow. I. *Trans. Linn. Soc. N. Y.* **4**: 247 pp.

————. 1938. The biological significance of bird weights. *Bird-Banding* **9**: 1-11.

————. 1946. Weights of resident and winter visitant Song Sparrows in central Ohio. *Condor* **48**: 41-42.

OAKESON, B. B. 1953. Cyclic changes in liver and spleen weights in migratory White-crowned Sparrows. *Condor.* **55**: 3-16.

ODUM, E. P. 1949. Weight variations in wintering White-throated Sparrows in relation to temperature and migration. *Wilson Bull.* **61**: 3-14.

————. 1958. The fat deposition picture in the White-throated Sparrow in comparison with that in long-range migrants. *Bird-Banding* **29**: 105-108.

————, and J. D. PERKINSON. 1951. Relation of lipid metabolism to migration in birds; seasonal variations in body lipids of the migratory White-throated Sparrow. *Physiol. Zool.* **24**: 216-230.

OWEN, D. F. 1954. The winter weights of titmice. *Ibis* **96**: 299-309.

PALMGREN, P. 1944. Studien über die Tagesrhythmik gekäfigter Zugvögel. *Zeits. Tierpsychol.* **6**: 44-86.

PICHOTKA, J. 1952. Das Verhalten der Schilddrüse und der Körpertemperatur bei der Adaptation an niedere Umgebungstemperaturen. *Arch. exper. Path. u. Pharmakol.* **215**: 299-316.

PRECHT, H., J. CHRISTOPHERSEN, and H. HENSEL. 1955. Temperatur und Leben. Springer, Berlin. 514 pp.

RAYNOR, G. S. 1956. Meterological variables and the northward movement of nocturnal land bird migrants. *Auk* **73**: 153-175.

ROWAN, W. 1925. Relation of light to bird migration and developmental changes. *Nature* **155**: 494-495.

————. 1929. Experiments in bird migration. I. Manipulation of the reproductive cycle: seasonal histological changes in the gonads. *Proc. Boston Soc. Nat. Hist.* **39**: 151-208.

SABINE, W. S. 1949. Dominance in winter flocks of Juncos and Tree Sparrows. *Physiol. Zool.* **22**: 64-85.

————. 1955. Winter society of the Oregon Junco: the flock. *Condor* **57**: 88-111.

————. 1956. Integrating mechanisms in winter flocks of Juncos. *Condor* **58**: 338-341.

SALOMONSEN, F. 1955. The evolutionary significance of bird migration. Det Kongelige Danske Videnskabernes Selskad, *Biol. Med.* **22**: 1-62.

SARGENT, T. D. 1959. Winter studies on the Tree Sparrow, *Spizella arborea. Bird-Banding* **30**: 27-37.

SAUER, F. 1957. Die Sternenorientierung nächtlich ziehender Grasmücken *(Sylvia atricapilla, borin* und *curruca).* Zeits. Tierpsychol. **14**: 29-70.

SCHILDMACHER, H. 1952. Stoffwechselphysiologische Studien am männlichen Gartenrotschwänzen *Phoenicurus ph. phoenicurus* (L.). *Biol. Zentralbl.* **71**: 238-251.

————. 1956. Physiologische Untersuchungen am Grünfinken *Chloris chloris* (L.) im künstlichen Kurztag und nach "hormonaler Sterilisierung." *Biol. Zentralbl.* **75**: 327-355.

————. 1958. Über Hemmung der Mauser auslösenden Wirkung des Thyroxins durch Testosteronpropionat beim Grünfinken, *Chloris chloris* (L.). XII Congr. Int. Orn., Helsinki, Abstr.: 26.

————, and L. Steubing. 1952. Untersuchungen zur hormonalen Regulierung des Fettwerdens der Zugvögel in Frühjahr. *Biol. Zentralbl.* **71**: 272-282.

SCHOLANDER, P. R., R. HOCK, V. WALTERS, and L. IRVING. 1950. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation and basal metabolic rate. *Biol. Bull.* **99**: 259-271.

SCHÜZ, E. 1952. Vom Vogelzug. Grundriss der Vogelzugskunde. Paul Schöps. Frankfurt/Main. 231 pp.

SEIBERT, H. C. 1949. Differences between migrant and non-migrant birds in food and water intake at various temperatures and photoperiods. *Auk* **66**: 128-153.

SNEDECOR, G. W. 1956. Statistical Methods. 5th ed. Iowa State College Press, Ames. 534 pp.

STEINBACHER, J. 1951. Vogelzug und Vogelzugforschung. Waldemar Kramer, Frankfurt/Main. 184 pp.

STEWART, P. A. 1937. A preliminary list of bird weights. *Auk* **54**: 324-332.

WAGNER, H. O. 1930. Über Jahres- und Tagesrhythmus bei Zugvögeln. *Zeits. vergl. Physiol.* **12**: 703-724.

————. 1956. Die Bedeutung von Umweltfaktoren und Geschlectshormonen für den Jahresrhythmus der Zugvögel. *Zeits. vergl. Physiol.* **38**: 355-369.

WALLGREN, H. 1954. Energy metabolism of two species of the genus Emberiza as correlated with distribution and migration. *Acta Zool. Fenn.* **84**: 1-110.

WEISE, C. M. 1956. Nightly unrest in caged migratory sparrows under outdoor conditions. *Ecology* **37**: 274-287.

WETHERBEE, H. B. 1934. Some measurements and weights of live birds. *Bird-Banding* **5**: 55-64.

WOLFSON, A. 1940. A preliminary report on some experiments on bird migration. *Condor* **42**: 93-99.

—————————. 1942. Regulation of spring migration in Juncos. *Condor* **44**: 237-263.

—————————. 1945. The role of the pituitary, fat deposition and body weight in bird migration. *Condor* **47**: 95-127.

—————————. 1954a. Weight and fat deposition in relation to spring migration in transient White-throated Sparrows. *Auk* **71**: 413-434.

—————————. 1954b. Body weight and fat deposition in captive White-throated Sparrows in relation to the mechanisms of migration. *Wilson Bull.* **66**: 112-118.

—————————. 1954c. Production of repeated gonadal, fat and molt cycles within one year in the Junco and White-crowned Sparrow by manipulation of day length. *J. Exp. Zool.* **125**: 353-376.

ZEIDLITZ, O. 1926. Vogelgewichte als Hilfsmittel für die Biologische Forschung. *J. Ornithol.* **74**: 296-308.

Hatheway School of Conservation Education, Mass. Audubon Society, Drumlin Farm, So. Lincoln, Mass.

RECENT LITERATURE

BANDING

(See also numbers 13, 18, 43)

1. Night-Lighting: A Technique for Capturing Birds and Mammals. Ronald F. Labisky. 1959. *Illinois Natural History Survey Biol. Notes*, No. 40: 11 pp. Bright lights were used at night to temporarily blind pheasants *(Phasianus colchicus)* and certain other animals until they could be captured in a hand net. Hay and stubble fields were cruised slowly in a panel truck equipped with floodlights and spotlights. When a roosting bird was observed, the floodlights were switched off and a hand-held spotlight focused on the bird. The netter, seated on the right front fender of the truck, jumped off and attempted to net the bird from the spotlighted side. Pheasants were difficult to capture by this technique until they had been roosting for 3 to 4 hours. After midnight netting was much more effective. Fog, rain, heavy dew, and frost resulted in pheasants holding tight, whereas during strong winds and snow the birds flushed more readily.

About one in three netting attempts resulted in the capture of a pheasant. Other species readily netted by this method were: Sora Rail *(Porzana carolina)*, Virginia Rail *(Rallus limicola)*, Barn Owl *(Tyto alba)*, Vesper Sparrow *(Pooecetes gramineus)*, and Grasshopper Sparrow *(Ammodramus savannarum)*.

An earlier use of similar techniques, in Louisiana, was described by E. A. McIlhenny *(Bird-Banding*, **13**: 19-28, January, 1942.)—F. C. Bellrose.

MIGRATION

(See also numbers 38, 58, 65, 66)

2. Bird-Migration Terms. D. Lack and K. Williamson. 1959. *Ibis*, **101**(2): 255-256. For intelligible discussion of modern migration research such as the radar studies reviewed in this issue, we have need of a more precise vocabulary. Recently several British ornithologists have agreed upon pertinent terms and definitions.

Brief paraphrases of their decisions follow. *Heading*—the direction in which the flying bird is pointing. *Track*—the actual path of the bird (the resultant of its heading and the action of the wind). *Diversion-line*—a replacement for "leading line," "guiding line," and "containing line." *Reversed migration*—general movement, not primarily related to a diversion-line, in a direction opposite to the seasonally normal one. *Retromigration*—movement turned in a direction opposite to normal by a diversion-line. *Drift*—displacement from the normal route by the wind. *Lateral displacement*—the drift of a bird maintaining a constant heading in a cross wind. *Disoriented drift*—the displacement of a