

TENTATIVE FIELD ESTIMATES OF METABOLISM IN BUNTINGS*

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INTRODUCTION

ANIMALS are characterized by their heterotrophic mode of nutrition. In spite of the adaptive diversity in feeding methods of animals and the variety of foods utilized, all food has this in common: it contains stored energy and the "building blocks" essential for life. Whereas an ecologist is interested in the types of food eaten and the processes of its procurement, a physiologist is interested in what happens to that food once ingested. To both, food is an important carrier of energy: to the ecologist as part of the energy flow within an ecosystem; to the physiologist as the source of energy-rich chemical bonds available to the organism to do work.

To measure energetic processes in birds, students of metabolism usually employ methods of indirect calorimetry. One widely used indirect measurement is based upon determinations of respiratory exchange of O_2 and CO_2 with calculations of proper thermal equivalents reflecting heat production. A second indirect measurement is based upon determinations of food consumption and energy balance with calorimetric conversions reflecting the energy available for heat production. Although both methods are designed to estimate the energy turnover in an organism, they differ somewhat in their adaptability and sensitivity in measuring certain fractions of this turnover. Because of this, some of the results obtained by these two methods cannot be compared precisely. However, both approaches are valuable and may be used to answer various important energetic questions (for details and discussion, see Davis, 1955; Kendeigh, 1949; King and Farner, 1961; Kleiber, 1961; Seibert, 1949; and Wallgren, 1954).

Metabolism in Free-living Birds. Both methods of animal calorimetry require that individuals be caged. No satisfactory method of measuring energy metabolism in wild birds under field conditions has been used, although the D_2O^{18} method of Lifson, Gordon, and McClintock (1955) seems promising. The lack of field methods for studying these energy exchanges or "bioenergetics" is of concern because laboratory housing modifies the environment, often in ways not immediately apparent. This is particularly true of the biological, as opposed to the physical, environment. Also, studies of the annual cycle in several species of buntings

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have suggested that there are certain differences in the bioenergetics of captive and wild birds (Helms, 1960). I have, therefore, attempted to develop an indirect calorimetric method to estimate metabolism in wild populations.

This attempt is predicated upon the premise that diel variations in body weight and visible fat, both of which can be determined in live birds under field conditions, reflect bioenergetic processes. This premise is supported by varied evidence (Odum and Perkinson, 1951; Farner, 1960; Helms and Drury, 1960), but problems arise in interpreting these bioenergetic processes and in relating them quantitatively to diel variations in energetic reserves.

To simplify the problems involved, we might assume that food is metabolized as rapidly as it can be eaten, digested, and assimilated from the digestive tract (i.e., there is no change in the energetic reserve nor in the composition of the body). In this case, body weight remains constant and equals tissue weight plus gut contents. Since energy is required to maintain vital metabolic processes and, in a homeotherm, body temperature, food must be constantly available and ingestion must be relatively continuous. This situation is approached by the smallest shrews, but not by the smallest birds (see Pearson, 1950).

Because most birds are diurnal in habit and do not feed at night, this model is not applicable. In addition to food eaten, digested, assimilated, and metabolized directly, diurnal birds must obtain a surplus over and above their immediate requirements, which can be stored as a reserve to be metabolized nocturnally when feeding is prevented by darkness. In small passerines, digestion and the elimination of fecal waste are rapid processes. Seed food passes through the entire gut in less than three hours (Wallgren, 1954), so that gut storage is insufficient and probably minor. The logical alternative to gut storage is storage of assimilated food molecules within the body in a relatively accessible form. Glycogen and fat are storage products of this type. Thus, a bird must acquire sufficient food during the daylight hours to meet its operating needs plus a surplus which can be stored as carbohydrate and/or lipid for nocturnal utilization. Therefore, body weight and composition cannot remain constant throughout the day, but rather must increase diurnally and decrease nocturnally with a respective increase and decrease in stored bioenergetic reserves. Gut contents and water content of the tissues also affect body weight, contributing a non-energetic component to diel fluctuations. If the relative contributions of these factors, energetic and non-energetic, can be separated, and if a bird is in material and energy balance during the period of analysis, fluctuations in the bioenergetic reserves could be used to make crude estimates of heat production.

This oversimplified model is best explained by a hypothetical example. Suppose Bird X averages 20 g and varies 2 g per day. Of this diel variation, 1 g is due to changes in non-energetic components and 1 g to changes in bioenergetic reserves. This means that Bird X weighs 19 g in the morning before feeding and 21 g in the evening before roosting. If we take 7.0 kcal/g as an energetic equivalent for stored reserves (King, 1961) and if the bird is in material and energy balance, Bird X uses 7.0 kcal overnight. Since small birds normally sleep at night and are in a post-absorptive condition for most of the night, this value approaches a resting metabolism for the night insofar as ambient temperature approaches the zone of thermal neutrality. If day and night are both 12 hours long, the value 14.0 kcal likewise approaches a resting metabolism for 24 hours. Diurnal activity necessary for the procurement of food, reproduction, and other major activities would not be reflected in caloric estimates obtained in this way since the bird could obtain energy for its performance directly from food, although thermoregulatory-effected departures from resting metabolism would be included. Therefore, metabolic estimates arrived at in this manner should fall between resting metabolism and existence energy, the energy needed for all basic maintenance activity (see Kendeigh, 1949).

By extending this model from an individual to a population, one should be able to make metabolic estimates for that population which would be as reliable and free from bias as the samples were. This model allows field data obtained from wild, free-living populations to be used.

METHODS

As part of a joint laboratory and field study of the annual cycle in buntings (Subfamily Emberizinae), I trapped many individuals in eastern Massachusetts between 1956 and 1960. Data from five species are presented in this paper: Tree Sparrow, *Spizella arborea*; Slate-colored Junco, *Junco hyemalis*; Song Sparrow, *Melospiza melodia*; White-throated Sparrow, *Zonotrichia albicollis*; and Fox Sparrow, *Passerella iliaca*.

Routine banding methods were used in sampling: all individuals were weighed to the nearest 0.1 g; time was recorded to the nearest five minutes; wing, tarsal, and tail measurements were taken; age and sex were determined when possible; molt was noted; and injuries and other abnormalities were recorded. Visible fat was determined by the method of Helms and Drury (1960).

Data from these samplings have been treated statistically. Sample sizes vary widely and, consequently, the reliability of estimates based upon them also varies. There is a marked seasonal bias.

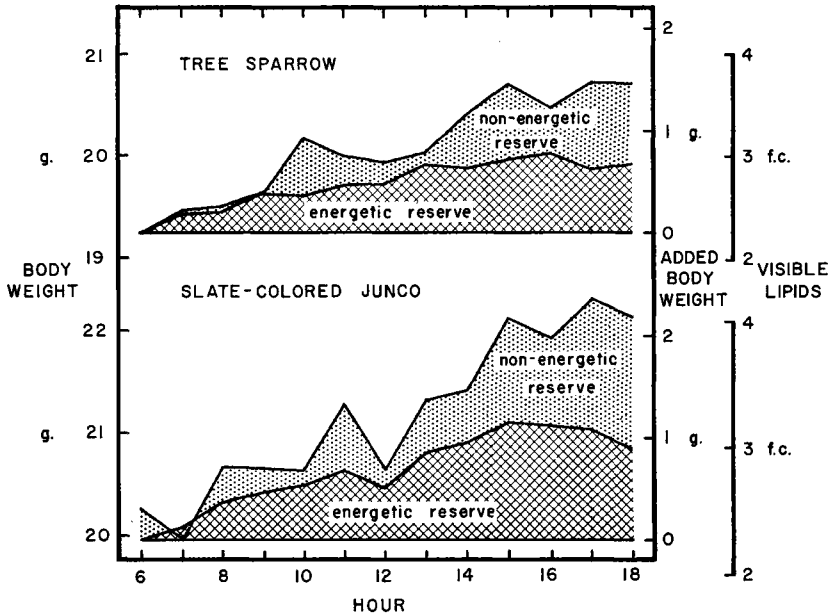


Figure 1. Diurnal increases in body weight and visible fat class in the Tree Sparrow and Slate-colored Junco (see also text). Mean body weight for hourly samples (scale on left) and mean body weight added to the minimal hourly mean during the day (inner scale on right) are indicated by the upper line for each species in this figure. Mean visible fat class (f.c.) for hourly samples (outer scale on right) is indicated by the middle line. Fat and weight scales are adjusted for both species so that body weight represented by fat class can be read in grams. That portion of the increased mean weight represented by increased mean fat represents an energetic reserve and the difference between this reserve and the increased mean weight represents some portion of a non-energetic reserve, largely composed of gut contents. 0500 samples are very small and are omitted. Sample statistics for these species are plotted in Helms and Drury (1960).

Treatment of data and sample statistics as they relate to the model discussed above are presented in the following discussion.

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RESULTS

Sample means. Statistics from all samplings are presented in Table 1. These statistics describe each sample and indicate its variability.

TABLE 1*
SAMPLE STATISTICS: BODY WEIGHT (IN G) AND VISIBLE FAT (IN FAT CLASS UNITS)

<i>Species</i>	<i>Mean weight</i>	<i>Standard deviation</i>	<i>Coefficient of variation</i>	<i>Range</i>	<i>Mean fat</i>	<i>Number of weights</i>	<i>Number of fat determinations</i>
<i>Spizella arborea</i>	20.12 ± 0.04	1.59	7.91	9.9	2.76	1,785	1,611
<i>Junco hyemalis</i>	21.16 ± 0.07	1.92	8.79	10.4	2.84	856	797
<i>Melospiza melodia</i>	22.30 ± 0.17	2.11	9.46	10.3	1.96	148	143
<i>Zonotrichia albicollis</i>	27.15 ± 0.14	2.66	9.80	12.7	2.70	347	346
<i>Passerella iliaca</i>	41.32 ± 0.23	3.66	8.86	17.2	2.67	245	243

* In this and in subsequent tables, the species are listed in order of increasing body weight.

The Song Sparrow sample is small and includes few afternoon weights: subsequent calculations for this species are questionable. The Tree Sparrow sample is most satisfying owing to its size and relative freedom from seasonal bias.

Diurnal variation. Body weight and visible fat of these birds vary characteristically during the day, somewhat as suggested by the model above (see Figure 1). Diurnally, the weight of an individual increases proportionately to food intake and energetic storage (more precisely, to the food, water, and indigestible materials within the alimentary tract, increases in tissue fluids and anabolic processes of all types, balanced by pulmonary, dermal and anal losses of material and catabolic processes of all types). Nocturnally, the weight of an individual decreases proportionately to gut evacuation and the utilization of energetic reserves (more precisely, to all material losses and catabolic processes of all types). A bird is in material and energy balance when diurnal gains balance nocturnal losses, thereby maintaining a constant body weight and composition. However, individual variations cannot be determined from population samples. It must be assumed that average or population diurnal increases reflect individual trends and are balanced by nocturnal losses, i.e., that the population statistics apply equally to individuals and that the population is in material and energy balance. The latter assumption is not strictly true, because body weight does vary seasonally, and the present samples are not free from seasonal bias. However, without the introduction of a time factor into the analysis, balance cannot be evaluated from the data at hand. Considering this and other uncertainties in this study, the assumption of balance does not appear to be untenable and does simplify the analysis.

TABLE 2
SAMPLE STATISTICS: DIURNAL INCREASES IN BODY WEIGHT (IN G) AND VISIBLE FAT
(IN FAT CLASS UNITS)

PART A					
<i>Morning minima (M) and afternoon maxima (A)</i>					
<i>Species</i>	<i>Hour</i>	<i>Mean weight</i>	<i>Standard deviation</i>	<i>Sample size</i>	<i>Mean fat</i>
<i>Spizella arborea</i>	0600	19.24 ± 0.21	1.12	28	2.25
	1700	20.71 ± 0.11	1.49	197	3.02
<i>Junco hyemalis</i>	0700	19.96 ± 0.20	1.45	53	2.27
	1700	22.34 ± 0.34	2.00	34	3.21
<i>Melospiza melodia</i>	0500	20.38 ± 0.39	1.44	14	1.16
	1400	24.43 ± 1.00	2.44	6	2.72
<i>Zonotrichia albicollis</i>	0600	25.59 ± 0.45	2.25	25	2.19
	1700	29.65 ± 0.60	2.33	15	3.34
<i>Passerella iliaca</i>	0600	38.54 ± 0.82	2.83	12	1.98
	1200	42.56 ± 0.95	4.16	19	3.01

PART B				
<i>Species</i>	<i>Diurnal increase</i>		<i>Diel relationship (in g/ fat class)</i>	<i>Diel weight variation as per- centage of mean</i>
	<i>Weight difference (A-M)</i>	<i>Fat difference (A-M)</i>		
<i>Spizella arborea</i>	1.47 ± 0.24	0.77	1.91	7.31
<i>Junco hyemalis</i>	2.38 ± 0.40	0.94	2.53	11.25
<i>Melospiza melodia</i>	4.05 ± 1.07	1.28	3.16	18.16
<i>Zonotrichia albicollis</i>	4.06 ± 0.75	1.15	3.53	14.95
<i>Passerella iliaca</i>	4.02 ± 1.26	1.03	3.90	9.73

Diurnal increases in weight and fat are shown in Table 2. These are the differences between the highest afternoon and lowest morning hourly sample means, calculated from all data taken within the indicated hours (the hour of minimal or maximal mean visible fat is not necessarily the same as that for weight, but is in most cases). It should be noted that individuals included in the morning and afternoon samples are usually different, but that individual repeats tend to verify the mean pattern of weight variation in Tree Sparrows (Helms and Drury, 1960). Inter-relations of weight and fat variations are also indicated in this table. (Although species values for diel relationship increase with increasing species mean weight, the trend is significant neither linearly nor curvilinearly [$P = 0.1-0.5$]: this may be related to different patterns of fat deposition [see Figure 2] and/or it may reflect seasonal biases. Further studies of patterns of fat deposition such as that of Odum and Perkinson [1951] are needed.)

TABLE 3*
 SAMPLE STATISTICS: BODY WEIGHT (IN G) IN RELATION TO FAT CLASS
 (IN FAT CLASS UNITS)

<i>Species</i>	<i>Fat Class</i>				
	1	2	3	4	5
<i>Spizella arborea</i>	18.04 ± 0.26 1.38 (28)	19.40 ± 0.06 1.45 (533)	20.36 ± 0.05 1.53 (993)	21.12 ± 0.12 1.54 (161)	
<i>Junco hyemalis</i>	19.21 ± 0.14 0.98 (51)	19.86 ± 0.08 1.25 (244)	21.28 ± 0.09 1.67 (332)	22.55 ± 0.12 1.65 (181)	24.14 ± 0.39 1.61 (17)
<i>Melospiza melodia</i>	21.05 ± 0.20 1.40 (51)	22.34 ± 0.28 1.97 (51)	23.44 ± 0.30 1.80 (37)	25.47 ± 0.84 2.23 (7)	
<i>Zonotrichia albicollis</i>	24.27 ± 0.28 1.85 (42)	25.72 ± 0.18 2.08 (138)	27.31 ± 0.17 2.02 (146)	29.80 ± 0.24 2.06 (75)	32.90 ± 0.52 2.91 (31)
<i>Passerella iliaca</i>	37.08 ± 0.71 3.01 (18)	40.14 ± 0.30 2.95 (94)	42.25 ± 0.33 3.38 (108)	44.31 ± 0.40 2.35 (34)	

* All weights (mean weight ± standard error) are grouped by fat class. The first value in the second line for each class sample is the standard deviation (with sample size in parentheses). These data are plotted in Figure 2.

Data in Table 2 are insufficient for an estimation of metabolism. Information about the lipids represented by visible fat class data is needed.

Visible fat in relation to body weight. All weight data used in preparing Table 1 have been separated by visible fat class. Statistics for the respective classes are presented in Table 3 and Figure 2. The following regression equations fit these mean data and correlations for all species are significant at the 1 per cent level: Tree Sparrow, $W = 17.18 + 1.02 F$; Slate-colored Junco, $W = 17.73 + 1.23 F$; Song Sparrow, $W = 19.49 + 1.44 F$; White-throated Sparrow, $W = 23.73 + 2.13 F$; Fox Sparrow, $W = 35.00 + 2.38 F$; where W = body weight in grams and F = visible fat in fat class units. In spite of the goodness of fit of these linear equations, the equation $W = 24.37 + 0.33 F + 0.30 F^2$ is significantly different from the linear equation for the White-throated Sparrow ($P = 0.05-0.01$), suggesting that the relationship is actually curvilinear and better represented by the polynomial. This might be expected because visible fat determinations are related to surface, while total body lipids, as reflected by body weight, are related to volume. However, the linear values are significant and will be used pending a reanalysis. The difference in the calculated fat-free weight, indicated by the first numerical value in the equations, should not be of major importance in the present context. (Note also the different relationships shown in Figure 2 by the different species: fat class five is extremely rare in Tree, Song, and Fox sparrows [one record for the

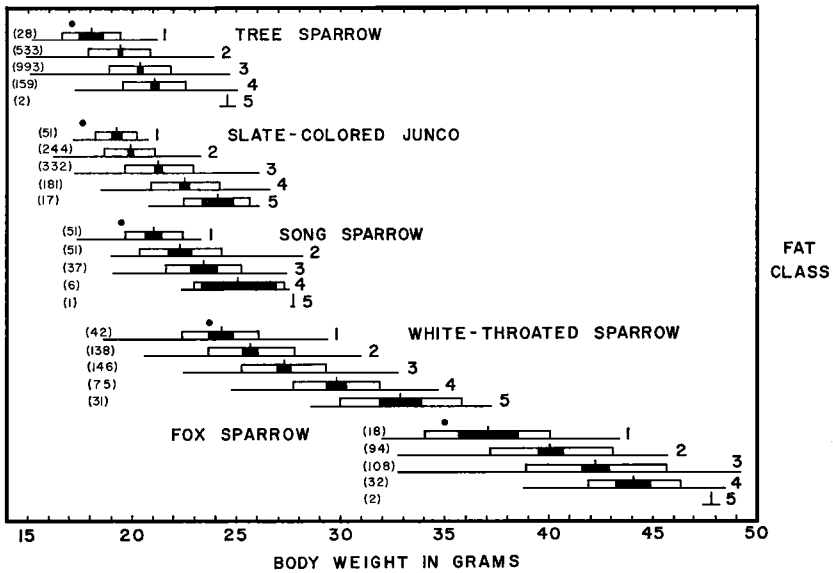


Figure 2. Body weight in relation to fat class. Statistics on body weight by fat class are plotted by species. The horizontal lines represent the ranges of values for the samples and the vertical lines represent the means. Open rectangles show one standard deviation to each side of the means, and the black rectangles show two standard errors to each side of the means. Fat class is indicated by the large number to the right of each plot. The small number in parentheses to the left shows sample size. The black circle represents the calculated fat-free weight for each species (see text). Non-overlap of the black rectangles indicates that the compared means differ significantly from one another at the 5 per cent level. Although overlap is shown by fat classes 2 and 3, and 3 and 4 in the Song Sparrow plot, the means of these fat classes differ significantly by *t*-test ($P =$ respectively <0.001 and $0.025-0.010$). Data for the Tree Sparrow and Slate-colored Junco are from Helms and Drury (1960) and, for the remaining species, from Helms (1960).

Song Sparrow and two each for the Tree and Fox Sparrow are included in fat class four in Table 3 and Figure 2]. This is probably related to species-specific differences in patterns of variation in weight and fat [Helms, 1959].)

Differences between the mean weights represented by fat classes one through five are presented for each species in Table 4, Part A. These differences are averaged and given in Table 4, Part B, Column 1. The differences calculated from the regression equations above for each species (mean fat ± 0.5 f.c.) are given in Column 2. The close agreement of these columns and the second numerical value in the linear equations will be noted.

TABLE 4
BODY WEIGHT DIFFERENCE (IN G) IN RELATION TO FAT CLASS (IN FAT CLASS UNITS)
PART A

Species	Weight differences between fat classes			
	Classes 1-2	Classes 2-3	Classes 3-4	Classes 4-5
<i>Spizella arborea</i>	1.36 ± 0.27	0.96 ± 0.08	0.76 ± 0.13	
<i>Junco hyemalis</i>	0.65 ± 0.16	1.42 ± 0.12	1.27 ± 0.15	1.59 ± 0.41
<i>Melospiza melodia</i>	1.29 ± 0.34	1.10 ± 0.40	2.03 ± 0.89	
<i>Zonotrichia albicollis</i>	1.45 ± 0.34	1.59 ± 0.24	2.49 ± 0.29	3.10 ± 0.57
<i>Passerella iliaca</i>	3.06 ± 0.77	2.11 ± 0.45	2.06 ± 0.51	

PART B

Species	Mean weight difference (in g/fat class) (1)	Difference calculated by regression at mean fat (in g/fat class) (2)	Diel relationship (in g/fat class, from Table 2) (3)	Variation in weight of energy reserves per fat class as percentage of diel variation in weight per fat class [(1)/(3) × 100]
<i>Spizella arborea</i>	1.03	1.01	1.91	53.93
<i>Junco hyemalis</i>	1.23	1.22	2.53	48.62
<i>Melospiza melodia</i>	1.47	1.44	3.16	46.52
<i>Zonotrichia albicollis</i>	2.16	2.13	3.53	61.19
<i>Passerella iliaca</i>	2.41	2.38	3.90	61.79

At this point, a second assumption is required. This is that all samplings tabulated in Table 3 and in Table 4, Part A, and Table 4, Part B, Column 1, and utilized in calculating the regression equations and values in Table 4, Part B, Column 2, were randomly taken throughout the day; and, therefore, that variations in non-energetic components, particularly in gut contents, have been randomized between all fat classes and do not enter into these differences—in other words, that the weight-fat relations derived from Table 3 are basically bioenergetic ones.

Diel relationships of weight and fat variation are reproduced (from Table 2) in Table 4, Part B, Column 3. These values include all increases in weight during the day and are considerably larger than those derived from Table 3. This would be expected if the above assumption does not err very greatly. Percentages in Column 4 of Table 4, Part B, express this relationship and suggest that about one-half of the diurnal increase in body weight is due to an increased bioenergetic reserve in these buntings.

With these statistics and assumptions, it is now possible to arrive at tentative metabolic estimates based upon (1) the diurnal increase in

TABLE 5*
ESTIMATED DIURNAL VARIATION IN ENERGETIC AND NON-ENERGETIC RESERVES
BY WEIGHT (IN G)

Species	Diurnal variation		Mean difference in bio- energetic reserves (in g/ fat class) (3)	Calculated diurnal variation in total reserves	
	Weight (1)	Visible fat (in fat classes) (2)		Energetic (4)	Non- energetic (5)
<i>Spizella arborea</i>	1.47	0.77	1.03	0.79	0.68
<i>Junco hyemalis</i>	2.38	0.94	1.23	1.16	1.22
<i>Melospiza melodia</i>	4.05	1.28	1.47	1.88	2.17
<i>Zonotrichia albicollis</i>	4.06	1.15	2.16	2.48	1.58
<i>Passerella iliaca</i>	4.02	1.03	2.41	2.48	1.54

* Diurnal variations in weight and fat are from Table 2. Column 3 reproduces the mean differences from Table 4, B, Column 1. Variation in energetic reserves is calculated by multiplying diurnal variation in fat by the mean difference in weight per fat class. Diurnal variation in weight minus the preceding value gives the calculated variation in non-energetic reserves. See also Figure 1.

the bioenergetic reserve, and (2) the quantitative nature of this reserve.

Estimates of metabolism. Diurnal variations in weight are separated into their postulated energetic and non-energetic components, according to the assumptions made above, and are presented in Table 5. Energetic components are obtained by multiplying the diurnal increase in fat class units (Table 2) by the weight variation in energetic reserves represented by one fat class (Table 4). Non-energetic components of diurnal variation are the differences between the energetic components and diurnal weight increases. This method was also used to separate the hourly values for the species plotted in Figure 1.

Assuming that (1) samples were taken randomly from all periods of the year so that periods of light and dark average 12 hours and (2) variations in energetic components represent about 7.0 kcal/g (King, 1961), it is possible to calculate the metabolic estimates in kcal/bird/day presented in Table 6. Rates, in kcal/g/day, are derived from these values using fat-free weights obtained by regression and are given in Table 6.

It is impossible to homologize these metabolic rates with ones obtained by other methods. However, as suggested, they should fall somewhere between resting metabolic values and existence energy, *if* the assumptions made in the course of arriving at these rates are valid.

DISCUSSION

The crudeness of the metabolic estimates in Table 6 is apparent. Metabolic rate per gram of body tissue does not decrease with increasing

TABLE 6
METABOLIC ESTIMATES

<i>Species</i>	<i>Metabolic estimates (in kcal/bird/day)</i>	<i>Metabolic rates (in kcal/g/day)</i>	<i>Calculated fat-free weight (in g)</i>
<i>Spizella arborea</i>	11.06	0.64	17.18
<i>Junco hyemalis</i>	16.24	0.92	17.73
<i>Melospiza melodia</i>	26.32	1.35	19.49
<i>Zonotrichia albicollis</i>	34.72	1.46	23.73
<i>Passerella iliaca</i>	34.72	0.99	35.00

body size, although such a trend might not be expected in the weight series covered. It should be emphasized moreover that (1) the samples are variable and biased, several being very small with correspondingly large standard errors in the values of the means used to calculate diurnal increases in weight and fat; and (2) the methods of calculation rest on several tenuous assumptions. Although the assumptions cannot be further evaluated at present, several considerations of the source and nature of biases should be discussed.

A. *Day length.* The bioenergetic estimates in Table 6 have been calculated on the assumption that samples were not seasonally biased, and, therefore, that the lengths of day and night were equal. If, however, the species sample is separated into months of capture, and an average normal day length computed (Table 7, Column 1), it can be seen that this assumption is approximated by only two of the samples. In terms of the proposed model, corrections can be made for these day length biases, e.g., the Tree Sparrow estimate is based upon a 13.6 hour night and a 27.2 hour day. Corrections are given in Table 7, Column 2.

B. *Temperature.* An added bias might be introduced by seasonal variation in temperature. Average normal ambient temperatures calculated for each species by sample months are given in Table 7, Column 3. Helms and Drury (1960) show that body weight of wintering Tree Sparrows and Slate-colored Juncos varies inversely with ambient temperature and suggest that diel variation is more pronounced when temperature is lower. Heat production must increase in the face of lowered ambient temperature if body temperature is to be maintained. Precise corrections for temperature effects are not possible, but an approximation can be attempted.

Considering two species, the Slate-colored Junco and the White-throated Sparrow, for which laboratory data are available, the equations calculated by King and Farner (1961), including the data of Seibert (1949), permit an evaluation of expected metabolism in these two species, at different temperatures and photoperiods, according to the following formulae:

TABLE 7
METABOLIC ESTIMATES CORRECTED FOR SAMPLE BIASES

Species	Corrections for:							
	Day length		Temperature		Migration		Calculated resting metabolism (kcal/bird/day) (8)	
	Normal day length (hours) (1)	Metabolism (kcal/bird/day) (2)	Normal temperature (°C) (3)	Metabolism (kcal/bird/day) (4)	Birds in migratory period (per cent) (5)	Metabolism (kcal/bird/day) (6)		Coloric density of 4.0 kcal/g (kcal/bird/day) (7)
<i>Spizella arborea</i>	10.4	9.8	3.3	6.4	28	10.4	6.1	
<i>Junco hyemalis</i>	10.7	14.6	7.0	12.2	78	13.8	6.3	
<i>Melospiza melodia</i>	13.4	29.8	9.1	22.2	98	21.5	6.5	
<i>Zonotrichia albicollis</i>	12.3	35.6	12.8	30.6	92	28.7	7.4	
<i>Passerella iliaca</i>	11.9	34.5	6.7	26.5	97	28.4	9.8	

Slate-colored Junco, 10 hour photoperiod, $M = 0.91 - 0.0083 T$, 15 hour photoperiod, $M = 1.08 - 0.013 T$; White-throated Sparrow, 10 hour photoperiod, $M = 0.79 - 0.0062 T$, 15 hour photoperiod, $M = 0.93 - 0.0076 T$; where M = metabolism in kcal/g/day and T = temperature in °C. Utilizing the normal ambient temperatures for these two species and interpolating from the normal photoperiod values, the following expected metabolic rates are obtained for these species: Slate-colored Junco, 0.87 kcal/g/day or 18.41 kcal/bird/day; and White-throated Sparrow, 0.77 kcal/g/day or 20.91 kcal/bird/day. These values for the Slate-colored Junco compare favorably with those in Table 6, while field estimates for the White-throated Sparrow are 1.7 times those expected. Values for the latter species to 23 kcal/bird/day are recorded by Weise (1956) in migratory periods. Thus the metabolic estimates for both of these species are at least of the right order of magnitude. In addition, Weise (1956) gives winter values for Tree Sparrows ranging between 12 and 18 kcal/bird/day. These compare favorably with values in Table 6.

Considering all five species, tentative temperature corrections in the metabolic values from Table 6 may be made, assuming that the formulae above are generally applicable for other species ranging in body weight from about 17 to 35 g. These corrections are given in Table 7, Column 4.

C. *Migration*. It is generally conceded that a marked hyperphagia is characteristic of migratory individuals during periods of movement (Farner, 1955 and 1960). Body weight of migratory individuals is independent of ambient temperature (Helms and Drury, 1960), suggesting an internal control at this period. Caged birds feeding *ad libitum* show a marked increase in body weight as do certain, but not all, wild populations. Actual weight increases in caged animals at this period may be, in part or in some species, artifacts of abundant food, but an increased diel weight variation in captive and wild individuals is probably real (Helms, 1959, 1960; Helms and Drury, 1960). This implies that food intake as well as lipogenesis and lipolysis may be accelerated. The significant feature of migratory physiology is, in this context, an increased metabolism.

The proportion of each species sample taken in a migratory period is given in Table 7, Column 5. Assuming that metabolizable energy is increased about 1.2 times during migratory periods (calculation from experiment 1 of King, 1961), the seasonal bias resulting from migratory preparation may be corrected (Table 7, Column 6), although it is probable that metabolic increases during migration would vary from species to species depending upon their migratory habits.

A relatively large proportion of all but the Tree Sparrow sample is in migratory condition. This throws the assumption of energy balance into doubt. A positive energy balance associated with migratory preparation

would markedly increase metabolic estimates based upon the suggested model. The estimates for species samples containing large numbers of migratory individuals depart most from expected values, suggesting that this source of error is appreciable in those samples.

D. *Resting metabolism.* A comparison of the uncorrected estimates in Table 6 with calculated resting metabolic values provides the best statement of the error probable in each estimate, since the field values should approach resting values if the original model approaches a reasonable evaluation of energetic processes and if laboratory determinations of energetics approximate field conditions. Based upon the Brody-Proctor formula, including small birds as recalculated (1961) by King and Farner ($\log M = 80.1 + 0.659 \log W \pm 0.76$, where M = metabolism in kcal/bird/day and W = weight in kg), calculated resting values may be derived. These are given in Table 7, Column 8. Field values from Table 6 are respectively 1.8, 2.6, 4.0, 4.7, and 3.5 times these resting values. All of the uncorrected estimates are of the same order of magnitude as calculated resting values and all are less than five times greater than the resting values. Estimates corrected for day length, temperature, and migration are also of the same order of magnitude and estimates based upon the latter two corrections are within a factor of four of resting values.

Considering that values for metabolism two times the resting value are not uncommon for small birds at lowered temperatures (King and Farner, 1961), these crude field estimates are rather good ones. The estimate for the Tree Sparrow corrected for temperature (6.4 kcal/bird/day) compares favorably with the calculated resting value (6.1 kcal/bird/day). This sample is the largest of those considered in this paper and shows the least seasonal bias.

In addition, the temperature-corrected value for the Slate-colored Junco (12.2 kcal/bird/day) is less than two times the calculated resting metabolism (6.3 kcal/bird/day) in spite of the fact that nearly 80 per cent of the sample was taken during a migratory period and presumably had a positive energy balance.

Samples of other species are much smaller, are largely composed of migratory individuals, and should be expected to give overestimated metabolic values.

E. *Caloric density and weight loss.* Recent studies of the effects of caloric restriction upon men suggest that the caloric value (7.0 kcal/g) assigned to weight loss by King (1961) may be too high. Brozek *et al.* (1957), measured caloric densities of 4.3 and 4.7 kcal/g on 580 and 1010 kcal/day diets, while Iampietro *et al.* (1961), found densities of 3.9 and 4.1 kcal/g on 600 and 0 kcal/day diets. At 4.0 kcal/g, the field estimates in Table 6 would be markedly lowered (see Table 7, Column 7). These

estimates exceed calculated resting metabolism for each species by 1.0, 1.5, 1.5, 2.7, and 2.0 times respectively. The caloric density of weight loss in birds needs to be investigated.

CONCLUSIONS

It would seem that the model proposed in this paper is valid when properly applied to the analysis of adequate field data based upon large samples. The use of this method leads to estimates which are compatible with laboratory determinations when sampling errors and biases are considered, although it lacks a critical precision. Extraction studies of lipids, studies of diel variations in gut contents, and measurements of caloric density of weight loss in birds are needed. The limitation of sampling to resident phases of the annual cycle and an inclusion of a temporal analysis of balance would reduce the rather large contribution of migratory hyperphagia and positive energy balance to the estimates obtained.

It is tentatively concluded that (1) energetic processes in laboratory and field populations are quantitatively similar, and (2) the modifications in biological environment imposed upon captive birds are probably insignificant in their effects upon bioenergetic processes outside reproductive and migratory periods of the year.

Although precise field methods such as those of Lifson *et al.* (1955), would be desirable, many workers may not have access to the equipment and isotopic heavy water required. Meanwhile, much banding data is accumulating which could be analyzed by the method proposed herein and sampling could be planned with an analysis of this type in mind to eliminate much of the seasonal bias. Studies along these lines would add significance to banding activities which generally yield little information for the amount of time spent operating stations, could be carried out by amateurs, and could supplement laboratory studies which are necessarily based upon confined individuals.

The proposed method of indirect calorimetry should be applicable in both field and laboratory studies of bioenergetics in birds. This application would provide an essential continuity, often lacking, between the nutritional and metabolic studies of the physiologist and the energy flow studies of the ecologist. Whether the method can be given sufficient precision to justify the time required for sampling and analysis must, however, await further study.

SUMMARY

1. The need for field estimates of bioenergetic processes in birds is pointed out and a model from which such estimates can be made is suggested. This model is based upon diel fluctuations in body weight and fat class as they reflect bioenergetic processes.

2. Sample statistics on body weight and visible fat reserves for five species of buntings (Subfamily Emberizinae) are tabulated. Diurnal increases in weight and fat are given.

3. Body weight is analyzed in relation to fat class and mean differences between fat classes are presented for each species sample. These values are assumed to represent variation in energetic reserves, while total diurnal increases in body weight include non-energetic components. All samples are assumed to come from populations which are in material and energy balance.

4. Based upon diurnal increases and the quantitative nature of lipid reserves, metabolic estimates are made. These are as follows: Tree Sparrow, 11.06 kcal/bird/day; Slate-colored Junco, 16.24 kcal/bird/day; Song Sparrow, 26.32 kcal/bird/day; White-throated Sparrow, 34.72 kcal/bird/day; and Fox Sparrow, 34.72 kcal/bird/day. According to the proposed model, these values include all resting and thermoregulatory expenditures of energy, but not those expenditures related to diurnal activity. In other words, these estimates should be between resting metabolism and existence energy.

5. Sources of bias in the field samples are discussed and related to the metabolic estimates with tentative corrections. All uncorrected estimates are of the same order of magnitude and are within a factor of five of calculated values for resting metabolism. Corrected estimates for the Tree Sparrow and Slate-colored Junco agree well with calculated resting metabolism for these species. The large proportion of migratory individuals with a positive energy balance probably accounts for a majority of the errors in estimates for the Song, White-throated, and Fox sparrows. Other seasonal biases, small sample size, and sampling error probably account for the remainder. There is also some doubt as to the caloric density that should be assigned to weight loss.

6. Based upon this test with field data, the proposed model appears to be a valid calorimetric tool for use with wild populations.

LITERATURE CITED

- BROZEK, J., F. GRANDE, H. L. TAYLOR, J. T. ANDERSON, E. R. BUSKIRK, and A. KEYS. 1957. Changes in body weight and body dimensions in men performing work on a low calorie carbohydrate diet. *J. Appl. Physiol.*, **10**: 412-420.
- 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. Pp. 198-237 *in* Recent studies in avian biology (A. Wolfson, ed.) Urbana, Univ. Illinois Press.
- FARNER, D. S. 1960. Metabolic adaptations in migration. Pp. 197-208 *in* Proc. XIIth International Ornithological Congress. Helsinki 1958.

- HELMS, C. W. 1959. Song and Tree Sparrow weight and fat before and after a night of migration. *Wilson Bull.*, **71**: 244-253.
- HELMS, C. W. 1960. Activity patterns, energetics, and migration in birds: a study in ecology and physiology of the annual cycle. Unpublished thesis, Harvard University, Cambridge. 187 pp.
- HELMS, C. W., and W. H. DRURY, JR. 1960. Winter and migratory weight and fat. Field studies on some North American buntings. *Bird-Banding*, **31**: 1-40.
- IAMPIETRO, P. F., R. F. GOLDMAN, M. MAYER, and D. E. BASS. 1961. Composition and caloric density of weight loss during caloric restriction in cold. *J. Appl. Physiol.*, **16**: 624-626.
- KENDEIGH, S. C. 1949. Effect of temperature and season on energy resources of the English Sparrow. *Auk*, **66**: 113-127.
- KING, J. R. 1961. On the regulation of vernal premigratory fattening in the White-crowned Sparrow. *Physiol. Zool.*, **34**: 145-157.
- KING, J. R., and D. S. FARNER. 1961. Energy metabolism, thermoregulation and body temperature. Pp. 215-288 in *Biology and comparative physiology of birds*, Vol. II. (A. J. Marshall, ed.) New York, Academic Press.
- KLEIBER, M. 1961. *The fire of life*. New York, Wiley.
- LIFSON, N., G. B. GORDON, and R. MCCLINTOCK. 1955. Measurement of total carbon dioxide production by means of D_2O^{18} . *J. Appl. Physiol.*, **7**: 704-710.
- ODUM, E. P., and J. D. PERKINSON, JR. 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.
- PEARSON, O. P. 1950. The metabolism of hummingbirds. *Condor*, **52**: 145-152.
- 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.
- WALLGREN, H. 1954. Energy metabolism of two species of the genus *Emberiza* as correlated with distribution and migration. *Acta Zoologica Fennica*, **84**. 110 pp.
- WEISE, C. M. 1956. Nightly unrest in caged migratory sparrows under outdoor conditions. *Ecology*, **37**: 274-287.

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