

THE AUK

A QUARTERLY JOURNAL OF
ORNITHOLOGY

VOL. 77

JANUARY, 1960

No. 1

FAT-FREE WEIGHTS OF BIRDS*

CLYDE E. CONNELL, EUGENE P. ODUM, AND HERBERT KALE

OUR extensive studies of lipid deposition in birds (Odum and Perkinson, 1951; Odum and Connell, 1956; Odum, 1958, 1959) have shown that the fat-free weight, in marked contrast to the total live weight, is remarkably constant for a given species and sex. A migrating male Red-eyed Vireo (*Vireo olivaceus*), for example, may weigh from 16 to 28 grams, while the weight of the body minus the fat will vary but a gram or so from 15. The fat-free weight of birds of the same wing length is even more constant, regardless of the total live weight of the individuals.

Actually there are two "fat-free" weights to be considered. The *nonfat dry weight*, *lean dry weight*, or simply *lean weight* is the weight of the bird minus both the fat and the water. The *fat-free weight*, on the other hand, is the weight of the bird minus only the fat. Since there are small variations in water content, and also since dehydration of specimens may occur before fat extractions are made, the lean dry weight generally exhibits a somewhat smaller coefficient of variation than the fat-free weight. Consequently, the lean dry weight is better suited for analyses of basic differences due to age, sex, season, or any other factor. However, the fat-free weight is of greater interest to the bird bander or other investigator working with the living bird. As will be demonstrated in this paper, one can accurately calculate the amount of fat simply by subtracting the known fat-free weight from the total live weight of the individual.

Knowledge of fat-free weight is also important for other reasons. Serious errors of interpretation can result when certain rates or ratios are expressed in terms of the total weight in cases where fat content is subject to wide variations. Metabolic rate, mineral content, or uptake

* This study is a byproduct of ecological research supported by an AEC grant [contract AT (07-2)-10].

of radioactive isotopes are best considered in terms of the fat-free or lean weights. King (1958) has recently pointed out that opposite conclusions regarding metabolic rates could be drawn depending on the weight basis used. In the example cited, fat birds had a lower metabolic rate per gram total weight but a higher rate per gram fat-free weight than thin birds.

In this paper we shall first analyse in detail the fat-free weight of a single species, the Savannah Sparrow, and then present a table of average fat-free and lean weights of other species of migratory birds. Conclusions relating to the fat-free weight apply equally well to the lean dry weight.

FAT-FREE WEIGHT OF THE SAVANNAH SPARROW
(*Passerculus sandwichensis*)

In connection with studies on the Savannah Sparrow as a component of the "old-field ecosystem" (Norris and Hight, 1957; Odum and Hight, 1957), a total of 230 specimens have been extracted. Some of these were killed by striking television towers at Aiken, South Carolina, and Tallahassee, Florida, during fall migrations, while others were collected with mist nets at various times from October to May on the old fields of the Atomic Energy Commission Savannah River Plant area in Aiken and Barnwell counties, South Carolina. All specimens were carefully weighed, sexed, aged (in so far as possible by skull ossification), and then racially determined by Dr. Robert A. Norris (see Norris and Hight, 1957). Birds were kept frozen until extracted according to the following procedures (see Odum, 1959, for additional details): The bird was completely dehydrated in a vacuum oven and the total dry weight determined; the difference between the dry weight and the original fresh weight represented the water content. The dry residue was then extracted by two fat solvents (alcohol and ether) and a final weight, the lean dry weight, determined. The fat-free weight was obtained by adding the weight of the water to the lean dry weight, and the value checked by subtracting the fat weight from the original wet weight. Let us now consider briefly various factors which might affect the fat-free weight.

Sex. The fat-free weight of males averaged significantly greater than that of females (see Table 2), but not when individuals of the same wing length were compared. For example, males with wings 68-69 mm. did not differ in weight statistically from females having the same wing lengths. In other words, males average heavier than females because they average larger in body size.

Age. When adults and immatures of the same sex and wing lengths were compared no significant differences in the fat-free weight were found. Twenty-two adults and 22 immatures with wings of 70-71 differed only 0.23 ± 0.25 , while 20 adults and 22 immatures with wings of 68-69 differed only 0.07 ± 0.30 .

Fat. When fat and thin birds of the same wing length and season were compared no significant differences in fat-free weight were found. Sixteen birds with wings 70-71 and a fat index less than 8 per cent (fat 8 per cent total live weight) differed only 0.03 ± 0.34 from 23 birds with the same wing measurements but with a fat index greater than 8 per cent. Likewise, fat and thin birds of wings 68-69 differed only 0.13 ± 0.37 .

Race. There were small differences in the average fat-free weights of the four races which winter commonly in the southeastern United States:

<i>P.s. savanna</i> (a large, light-colored race)	16.16 gms. (111 individuals)
<i>P.s. labradorius</i> (a large, dark race)	16.27 gms. (48 individuals)
<i>P.s. mediogriseus</i> (a medium-sized, light race)	15.38 gms. (53 individuals)
<i>P.s. oblitus</i> (a small, dark race)	15.01 gms. (16 individuals)

Two individuals of the rare *P.s. nevadensis* (a small, light race) averaged 14.92 grams. When birds of different races but having the same wing length were compared, no significant differences were found. It was evident that racial differences in weight are the result of differences in average body size.

Season. When individuals of same wing length taken in fall, winter, and spring were compared, it was found that the fat-free weight in fall was significantly lower than in the winter and spring. The magnitude of this difference is shown in Figure 1. Analysis of variance showed that the estimated variance between wing-length categories and also between fall and winter or spring was significantly greater than would be expected were samples from the same population. Weights in winter and spring did not differ significantly. While winter and spring birds were generally fatter than fall birds, fat as such apparently did not explain this difference (as indicated in the above paragraph). Perhaps carbohydrate or other nonfat reserves are depleted to a small extent in postmigratory birds. A portion of the fall sample was from television-tower kill, but there was no difference in fat-free weight between such birds and birds taken by mist nets in the old fields in October and November.

Wing length. As would be expected over-all body size as indicated by the wing length proved to be the most important factor influencing the fat-free weight. In fact, as indicated by the above analyses, no other factor except season need be considered; and seasonal differences

Figure 1A.

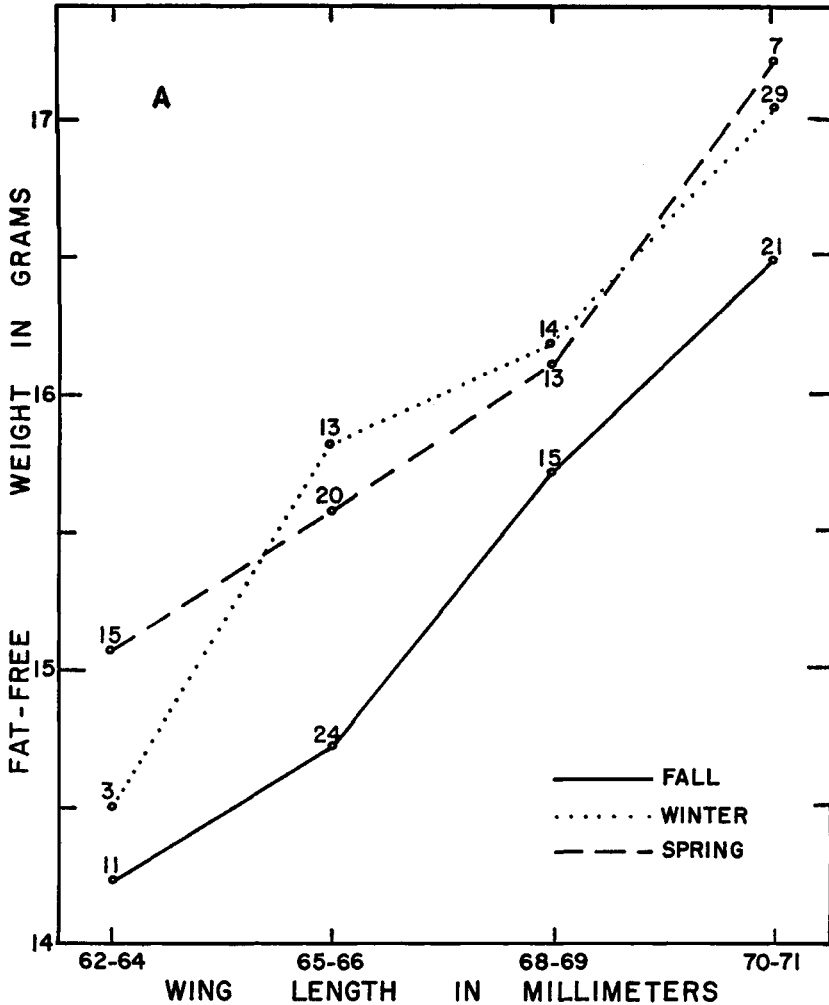


Figure 1. Fat-free weights of Savannah Sparrows in relation to wing length by seasons (upper graph, A) and for all 230 individuals on a semilog plot (lower graph, B). Numbers on curves in the upper graph are number of individuals.

TABLE 1

FAT-FREE WEIGHTS OF SAVANNAH SPARROWS (*Passerculus sandwichensis*)
OF DIFFERENT WING LENGTHS

Wing length mm.	Number of birds	Fat-free wt. in gms.	
		Actual values	Estimated from graph ¹
63	8	14.58	14.50
64	18	14.88	14.80
65	29	15.12	15.10
66	28	15.42	15.40
67	23	15.75	15.70
68	24	16.17	16.00
69	18	15.76	16.30
70	36	16.85	16.60
71	21	16.86	17.00
72	13	17.59	17.40

¹ Figure 1, lower curve.

are hardly great enough to be of concern to the bird bander. Accordingly, fat-free weights as function of wing lengths are plotted in Figure 1, both for seasons separately and for all of the 230 specimens together. The relationship appears curvilinear on the arithmetic plot and approaches a straight line in the semilog plot. In Table 1 average fat-free weights for each wing length are shown, together with values estimated from the smoothed curve (lower graph, Figure 1). Since the fat-free weight is a more precise measurement than the wing length, use of the figures from the smoothed curve are fully justified. The figures in the last column of Table 1 are best used in calculating the fat content of a living Savannah Sparrow. In general, the fat-free weight increases 0.30 grams for each mm. of wing length in small- and medium-sized birds, and 0.40 grams per mm. in large birds.

Figure 1B.

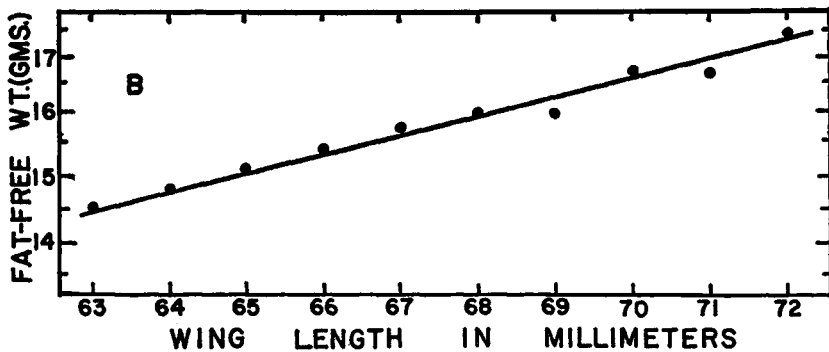


TABLE 2

CALCULATION OF BODY FAT CONTENT OF LIVING SAVANNAH SPARROWS
(*Passerculus sandwichensis*) BANDED AND RELEASED

Bander's observation ¹			Calculation of fat			
Date (1958)	Wing mm.	Live weight gms.	Fat class ²	Fat-free wt. ³ gms.	Gms. fat ⁴	Fat index ⁵ %
Sept. 9	63	16.9	0	14.5	2.4	14.2
Sept. 21	64	16.1	0	14.8	1.3	8.1
Oct. 4	67	20.3	0	15.7	4.6	22.7
Oct. 4	68	17.5	0	16.0	1.5	8.8
Sept. 20	66	17.7	1	15.4	2.3	13.0
Oct. 14	71	21.3	1	17.0	4.3	20.2
Feb. 17	65	17.0	1	15.4	1.6	9.4
Feb. 17	70	17.2	1	16.6	0.6	3.5
Sept. 20	64	19.4	2	14.8	4.6	23.7
Feb. 17	67	20.0	2	15.7	4.3	21.5
Feb. 17	65	20.0	3	15.1	4.9	24.5
Feb. 21	69	23.5	3	16.3	7.2	30.6
Feb. 21	70	20.5	3	16.6	3.9	19.0
Feb. 21	70	24.0	3	16.6	7.4	30.8
Feb. 21	69	21.9	4	17.0	4.9	22.4
Feb. 21	70	23.6	4	16.6	7.0	29.7

¹ Dr. James Baird, Norman Bird Sanctuary, Middletown, Rhode Island.² Fat condition as judged by external appearance (the McCabe index).³ From last column in Table 1.⁴ Live weight minus fat-free weight.⁵ Live weight/gms. fat \times 100.

CALCULATING THE AMOUNT OF FAT IN THE LIVING BIRD

Table 2 illustrates how the bird bander or experimental ornithologist could calculate the amount of fat in the living bird from the data on fat-free weight. Dr. James Baird has kindly sent us some data on Savannah Sparrows from his banding station in Rhode Island to use as an example. The live weights, wing measurements, and estimate of degree of fatness from superficial examination (*i.e.*, the McCabe, 1943, index) as shown in Table 2 are samples from his data; the estimated amount of fat for each individual was calculated by subtracting the fat-free weight (of appropriate wing length category as shown in last column of Table 1) from the live weight. We have also calculated a "fat index" as a percentage of estimated fat of live weight. It is evident that the calculated fat agrees only roughly with the observers' estimate of the degree of fatness. Note especially the wide variation in birds placed in classes "0" and "1" by the observer. Assuming that the calculated values are accurate, it would appear that estimates from superficial examination are most reliable in very fat individuals and

least reliable in the low and intermediate ranges where considerable amount of internal fat may not be visible.

FAT-FREE WEIGHTS OF OTHER MIGRATORY SPECIES

In Table 3 the fat-free and also lean dry weights are given for a number of migratory species. These data are based on television-tower-killed specimens, except for a portion of the Savannah Sparrows which, as already indicated, were taken with mist nets. The weight-wing

TABLE 3
AVERAGE FAT-FREE WEIGHTS AND STANDARD ERRORS OF THE MEAN
OF 14 SPECIES OF MIGRATORY BIRDS

<i>Species</i>	<i>Sex</i>	<i>Number individuals</i>	<i>Nonfat dry or lean wt. in gms.</i>	<i>Fat-free wt. in gms.</i>
Sora Rail <i>Porzana carolina</i>	female	7	17.08 ± 0.34	49.83 ± 0.42
Ruby-throated Hummingbird <i>Archilochus colubris</i>	male	9	0.64 ± 0.014	2.50 ± 0.11
	female	12	0.71 ± 0.017	2.76 ± 0.10
Swainson's Thrush <i>Hylocichla ustulata</i>	female	10	7.31 ± 0.12	26.22 ± 0.30
Red-eyed Vireo <i>Vireo olivaceus</i>	male	87	4.74 ± 0.034	15.05 ± 0.11
	female	91	4.66 ± 0.032	14.55 ± 0.12
Tennessee Warbler <i>Vermivora peregrina</i>	both	11	2.41 ± 0.063	7.94 ± 0.13
Magnolia Warbler <i>Dendroica magnolia</i>	both	8	2.37 ± 0.17	6.70 ± 0.40
Black-throated Blue Warbler <i>Dendroica caerulescens</i>	both	16	2.30 ± 0.084	7.64 ± 0.17
Bay-breasted Warbler <i>Dendroica castanea</i>	both	10	3.50 ± 0.11	9.88 ± 0.27
Bobolink <i>Dolichonyx oryzivorus</i>	male	10	8.60 ± 0.10	25.04 ± 0.98
	female	16	7.66 ± 0.18	22.92 ± 0.47
Scarlet Tanager <i>Piranga olivacea</i>	both	28	8.18 ± 0.10	23.52 ± 0.24
Summer Tanager <i>Piranga rubra</i>	male	19	8.47 ± 0.11	24.13 ± 0.40
	female	25	8.05 ± 0.10	23.87 ± 0.21
Indigo Bunting <i>Passerina cyanea</i>	male	37	4.20 ± 0.05	13.14 ± 0.18
	female	18	3.97 ± 0.04	12.46 ± 0.11
Savannah Sparrow <i>Passerculus sandwichensis</i>	male	108	5.13 ± 0.021	16.65 ± 0.07
	female	122	4.63 ± 0.020	15.27 ± 0.06
White-throated Sparrow <i>Zonotrichia albicollis</i>	male	9	7.49 ± 0.024	22.75 ± 0.14
	female	35	6.92 ± 0.006	21.24 ± 0.05

length relationship could, of course, be worked out for those species where large numbers of individuals have been extracted, but this refinement is not yet possible in many cases. Since the average fat-free weight of males and females differs in many species, separation by sexes is sufficient for most purposes. In species listed in Table 3 males generally average larger and heavier than females; female hummingbirds, however, are significantly heavier than males (see also Norris, Connell, and Johnston, 1957). The sexes were not separated in species where the number and/or weight differences were small. Additional material may, of course, show that a sex difference does exist in these species.

In summary, these data (Table 3) may be used to determine the approximate fat content of living or freshly collected birds, bearing in mind the following: (1) The fat content of individuals larger than average will be overestimated (since fat-free weight will be larger than average) and that of small individuals underestimated. If the wing measurement is taken at the time of banding or handling, a correction could easily be worked out based on trends shown in Figure 1 and Table 1. (2) Since most individuals on which Table 3 is based were taken during the fall migration the values may be slightly lower than at other seasons, assuming that the relationship with season demonstrated in the Savannah Sparrow also holds for other migratory species. (3) The data presumably are applicable to any individual which has completed its postjuvinal molt.

It should be emphasized that all the fat-free weights discussed in this paper refer to healthy birds. Starved or diseased birds may not only lose practically all of their fat, but their total weight could be less than the fat-free weight as given in Tables 2 and 3. If the fat-free weight drops more than a gram or so below the "normal" (as sometimes has happened in our captive birds), the bird rarely recovers; apparently too much of the vital "body" has been consumed. So far, all of the hundreds of television-tower-killed birds we have processed have appeared healthy with a minimum of 2 per cent and a maximum of about 50 per cent fat.

SUMMARY

The fat-free weight, and also the lean dry weight, is relatively constant for birds of the same size (as indicated by wing length) and species in marked contrast to the total live weight which, in migratory species, fluctuates greatly because of the large variations in fat deposits. Accordingly, the amount of body fat of the living bird, or fresh speci-

men, may be accurately calculated by subtracting the fat-free weight (as a previously determined constant) from the live weight. Detailed analysis of fat-free weights of 230 Savannah Sparrows showed that sex, age, and racial differences were entirely the result of differences in basic body size as indicated by wing length. Postmigratory individuals, however, exhibited a lower fat-free weight than wintering or pre-migratory individuals of the same size. Fat-free weight values for males and females would provide the bird bander with a basis for a reasonably good estimate of the fat level. For a more precise estimate, fat-free weights would need to be worked out for each wing-length category, or else corrections made for individuals larger or smaller than average for the species. A table of fat-free and lean dry weights of 14 species of migratory birds is included.

LITERATURE CITED

- KING, J. R. 1958. Review of: Rautenberg, Werner, Vergleichende Untersuchungen über den Energiehaushalt des Bergfinken (*Fringilla montifringilla*) und des Haussperlings (*Passer domesticus*)., J. für Orn., **98**: 36-64. 1957. Bird-Banding, **29**: 61-64.
- MCCABE, T. T. 1943. An aspect of collectors' technique. Auk, **60**: 550-558.
- NORRIS, R. A., C. E. CONNELL, and D. W. JOHNSTON. 1957. Notes on fall plumages, weights, and fat condition in the Ruby-throated Hummingbird. Wilson Bull., **69**: 155-163.
- NORRIS, R. A., and G. L. HIGHT, JR. 1957. Subspecific variation in winter populations of Savannah Sparrows: a study in field taxonomy. The Condor, **59**: 40-52.
- ODUM, E. P. 1958. The fat deposition picture in the White-throated Sparrow in comparison with that in long-range migrants. Bird-Banding, **29**: 105-108.
- ODUM, E. P. 1959. Lipid deposition in nocturnal migrant birds. Proc. XII International Ornithological Congress (in press).
- ODUM, E. P., and C. E. CONNELL. 1956. Lipid levels in migrating birds. Science, **123**: 892-894.
- ODUM, E. P., and G. L. HIGHT, JR. 1957. The use of mist nets in population studies of winter fringillids on the AEC Savannah River Area. Bird-Banding, **28**: 203-213.
- ODUM, E. P., and J. D. PERKINSON, JR. 1951. Relation of lipid metabolism to migration in birds: seasonal variation in body lipids of the migratory White-throated Sparrow. Physiol. Zool., **24**: 216-230.

Department of Zoology, University of Georgia, Athens, Georgia.