BODY CHARACTERISTICS OF PALM WARBLERS FOLLOWING AN OVERWATER FLIGHT

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On the drizzly overcast afternoon of 24 October 1965 approximately 35 small birds landed aboard the U. S. Coast Guard Cutter "Hollyhock" between 1400 and 1800 hours. The ship's position was 76° 20′ N, 21° 40′ W, or some 10 to 20 miles off the northeast coast of Cuba. Among the birds landing on the ship were 27 western Palm Warblers (*Dendroica p. palmarum*) that were captured and frozen by J. C. Dickinson, Jr. and Neil Payne of the Florida State Museum. These specimens, ultimately given to the author, provided needed data relating to bioenergetics of avian flight, fat deposits, and fat utilization. The geographic position, prevailing winds, and season indicated that the birds were on the verge of completing an extended overwater flight from the north. This appears to be the first unequivocal postflight sample of birds available for detailed fat studies, because samples heretofore reported in the literature as presumed postflight birds contained individuals that might have been aground for some time prior to collection (Odum, 1960; Odum *et al.*, 1964; Kuroda, 1964; Johnston and McFarlane, 1966). Unfortunately, because of the geographic location of the ship sample, it is impossible to state precisely where the overwater flight originated. These birds could have come directly from southern Florida or from any points along the Atlantic seaboard, perhaps via the Bahama Islands. Nonetheless, comparing body weights, fat quantities, and other characteristics of the ship sample with similar data from migrating Palm Warblers collected at Florida television towers during fall migration should help to clarify certain problems relating to flight bioenergetics and fat utilization.

Samples and Methods

Ted T. Allen and his associates furnished 30 frozen western Palm Warblers killed at a television tower in Jacksonville, Florida on 7–8 October 1964. From this Jacksonville sample and the ship sample, three body components (water, nonfat dry, and fat weights) were obtained by using techniques previously utilized (Johnston, 1962). The data from these two samples have been compared with values for 34 western Palm Warblers killed at a Tallahassee, Florida, television tower between 2 and 30 October (1956, 1957, 1960), which values were provided by Shirley Marshall at the University of Georgia. On 22 October 1965 another 26 western Palm Warblers were killed at the same Tallahassee tower and were given to me by Herbert L. Stoddard, Sr. This last group was not analyzed for fat; it is used here only for weight comparisons.

Some weights of autumnal migrant Palm Warblers are available in the literature (for Warner Robins Air Force Base, Georgia; Johnston and Haines, 1957). Other data were obtained as follows: 59 weights from coastal New Jersey (Murray and Jehl, 1964; Bertram G. Murray, Jr., pers. comm.); 231 weights from Massachusetts and

TABLE 1
WEIGHTS (IN GRAMS) OF PALM WARBLERS

Sample	*N*	*Mean* ± *S.E.*	*Extremes*
Massachusetts and Rhode Island			
18–30 September	140	10.7 ± 0.09	7.8–14.4
1–15 October	90	10.8 ± 0.11	8.1–13.3
New Jersey 25 August–20 October 1960	59	9.8 ± 0.12	7.9–12.3
Bermuda 8–27 October	10	9.3 ± 0.24	8.3–10.3
Jacksonville, Florida 7–8 October 1964	30	10.2 ± 0.18	8.4–12.6
Ship sample, 76° 20′ N, 21° 40′ W 24 October 1965	27	8.4 ± 0.11	7.1– 9.4
Champaign County, Illinois 6–7 October 1955	25	10.4 ± 0.17	8.6–12.5
Warner Robins Air Force Base, Georgia 7–8 October 1954	13	10.4 ± 0.19	9.3–11.8
Tallahassee, Florida			
2–30 October	34	11.2 ± 0.17	9.2–13.6
22 October 1965	26	12.1 ± 0.21	9.6–13.9

Rhode Island from James Baird and his associates; 25 weights from a television tower in Champaign County, Illinois from Richard Brewer; and 10 weights from Bermuda from David B. Wingate. Data for these birds are shown in Table 1.

RESULTS AND DISCUSSION

It is instructive to compare weights and fat contents of migrating Palm Warblers (Table 1) and the data presented by Odum (1965) and Caldwell *et al.* (1963). The latter investigators compared fat levels for certain migrants killed at a Michigan television tower with others killed at the Tallahassee television tower. Although no Palm Warblers were included, the mean fat levels in autumn for seven tropical-wintering thrushes, warblers, tanagers, and vireos were significantly greater in Florida than in Michigan. The data in Table 1 indicate a similar increase in autumnal body weights in Palm Warblers between Illinois and Florida. The mean fat index (fat as a proportion of the nonfat, dry weight) of trans-Gulf migrants studied by Caldwell *et al.* (1963) was 1.6, as compared with a mean of 0.95 for the Tallahassee Palm Warblers. Because some of the Palm Warblers had fat indexes up to 1.6 (Table 2), some of them undoubtedly had sufficient fat stores to fly nonstop to Yucatan or Cuba whereas others did not; probably the latter birds would have overwintered in Florida.

Fat values from the ship sample (Table 2) serve to clarify some additional features of small migrant birds. Some authors have proposed that a certain quantity of fat is "reserve fat," or "tissue fat," which by definition is not catabolized during extended flights. Johnston (1965) assumed this

TABLE 2
BODY COMPONENTS OF PALM WARBLERS

Sample	*N*	*Body weight*	*Water*	*Nonfat dry*	*Fat*	*Fat index*
Jacksonville	30	10.19 ± 0.18[1]	5.28 ± 0.07	3.13 ± 0.06	1.79 ± 0.15	0.57 ± 0.05
		8.39 – 12.64[2]	4.57 – 6.10	2.64 – 3.68	0.53 – 3.66	0.18 – 1.25
Tallahassee	34	11.15 ± 0.17	5.76 ± 0.08	2.79 ± 0.03	2.66 ± 0.15	0.95 ± 0.05
		9.19 – 13.60	5.01 – 7.79	2.46 – 3.06	0.91 – 4.71	0.32 – 1.62
Ship	27	8.40 ± 0.11	5.35 ± 0.06	2.61 ± 0.04	0.43 ± 0.05	0.17 ± 0.02
		7.1 – 9.4	4.65 – 5.99	2.20 – 2.91	0.05 – 1.41	0.02 – 0.53

[1] Mean ± standard error, in grams.

[2] Extremes.

to be 1.0 g in the Indigo Bunting (*Passerina cyanea*), and Odum (1960: 571) stated that "the available energy for flight is calculated assuming that one-half gram of body fat is not available." It now appears that the 0.5 g value assumed by Odum was a reasonable estimate, at least for small migrants like Palm Warblers because in this species the mean weight of fat per bird in the ship sample was 0.43 g. Nevertheless some birds had extremely low fat contents, ranging down to 0.05 g per bird.

In a study similar to this one Kuroda (1964) obtained weights of the Dusky Thrush (*Turdus naumanni*) after a 425-mile flight across the Sea of Japan. Although his analysis of fat included only subcutaneous and abdominal deposits ("not including the amount in tissues"), he noted that many of the arriving thrushes were in an exhausted condition with no subcutaneous fat but others had up to 4 g of fat (5.8 per cent of body weight). Generally speaking some of those thrushes resembled the ship sample of Palm Warblers because the latter had fat quantities between 0.05 and 1.4 g.

The low fat quantities or fat index values of the ship sample raise another question. To what level can fat deposits be depleted before other body components, such as water and the nonfat dry contents, are affected? Odum *et al.* (1964: 1038) made one suggestion: "what seems to happen is that the nonfat portion of the body remains remarkably homeostatic as the fat is catabolized during long flights until a fat index of 0.3 to 0.2 is reached; below this level a decline in nonfat dry weight is observed suggesting that at least 0.2 g of fat per gram nonfat . . . can be used only at the expense of burning some of the non-fat tissue as well." Rogers and Odum (1964) proposed a similar level at which nonfat components start to be burned in a series of wood warblers. This level can now be tested quantitatively in Palm Warblers if one compares body component fractions of the Jacksonville sample with those of the ship sample. These samples show significant differences in body weight, fat, fat index, and nonfat dry weight, with the ship sample having the lower values. Water contents are not significantly different. At an average fat index of 0.17 in the ship sample the nonfat dry contents were being affected (catabolized?).

The question of dehydration has also arisen, especially because Yapp (1956: 317) suggested that "the limits of a long flight may well be set by thirst. . . ." Although the mean values for the ship sample versus the Jacksonville sample do not reveal a significant loss of water ($0.5 < P < 0.6$), certain individuals in the ship sample might have been slightly dehydrated. These birds, whose lean body weights (6.85, 7.17, and 7.35 g) were far below the sample mean of lean body weights (8.01 g), also had the lowest water weights. However only one of these three had a markedly low nonfat dry weight. Thus perhaps 2 individuals of the 26 birds could be considered dehydrated, although it would appear that any dehydration occurs only at extremely low body weight and that nonfat dry components are affected in extended flights before body water. LeFebvre (1964) noted that body water did not decrease greatly in homing pigeons undertaking flights of several hundred miles, and Nisbet *et al.* (1963) suspected that Blackpoll Warblers (*Dendroica striata*) lost little or no water during flight.

Avian flight bioenergetics is currently a controversial subject chiefly because experimental data are largely lacking, and probably none of the recent proposals on estimates of flight distances, for example, will prove to be 100 per cent correct. Odum (1965: 43) determined by indirect methods "that the average flight metabolic rate is about 0.26 kcal/g per hr . . ." in small migrating birds. Yet if one calculates basal rate of metabolism by an appropriate formula (King and Farner, 1961) and assumes that flight metabolic rate is approximately 8 times BMR (see LeFebvre, 1964; Lasiewski, 1963; Tucker, 1966), then a bird the size of a lean Palm Warbler (8.3 g) requires 1.12 kcal/hr in flight. Although the "Odum method" and "BMR method" have different bases, in order to compare them as closely as possible for Palm Warblers some common values have been employed: (1) flight speed is taken as 25 mph; (2) preliminary studies (Johnston, unpublished) from a small sample of warblers show the caloric value of migratory bird fat to be 9.39 kcal/g; (3) energy expenditure in flight is calculated from lean body weight, not total body weight; and (4) the calculations omit influences of head and tail winds in flight.

Maximum flight range capabilities are calculated for Palm Warblers in Table 3. In the long run the "Odum method" appears to be too conservative and the "BMR method" perhaps represents an upper limit, but evidence from the ship sample suggests that the "BMR method" is reasonably accurate. An observation on the condition of the Palm Warblers from the ship is pertinent. By no means were those birds so exhausted that they were necessarily in imminent danger of death or falling into the water. Some birds, after once alighting on the ship, escaped by flying off, and

TABLE 3
ESTIMATED FLIGHT RANGES OF PALM WARBLERS[1]

Sample	*"Odum method"*	*"BMR method"*
Jacksonville		
average individual (average fat-free body weight and fat weight)	195 miles	375 miles
fattest individual	398 miles	767 miles
Tallahassee		
average individual	290 miles	558 miles
fattest individual	513 miles	988 miles
Ship		
average individual	47 miles	90 miles
leanest individual	5 miles	11 miles

[1] Assuming a flight speed of 25 mph; 1 g fat yields 9.39 kcal; based on fat-free weights, not on total body weights.

many of those captured had to be chased vigorously through quarters below decks. This observation suggests that the minimum value of 5 miles, calculated by the "Odum method" for the leanest birds is too low; probably even the leanest ones could have flown the 10 or more miles to Cuba.

Furthermore observational evidence suggests that some Palm Warblers follow a trans-Gulf migratory route (Bullis, 1954; Stevenson, 1957), the minimum north Florida–Yucatan distance being approximately 650 miles. If this route had been the one taken by some of the Palm Warblers killed at the Tallahassee tower, calculations by the "Odum method" are again too low, even for the fattest individual.

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SUMMARY

From a ship passing 10 to 20 miles off the northeast coast of Cuba a sample of autumnal migrating Palm Warblers was obtained. This sample and one taken at a Jacksonville, Florida television tower were analyzed for fat and nonfat components, and the body components have been compared with those of other samples of autumnal migrating Palm Warblers.

Comparable fat data from a Tallahassee, Florida, sample provide indirect evidence that some Palm Warblers could pursue a trans-Gulf route to Yucatan. The ship sample contained birds with extremely low fat in-

dexes, down to 0.02, and suggest that, at a mean fat index of 0.17, nonfat dry body components were being catabolized even though these migrants had lost little or no water.

Estimations of flight ranges were calculated by two methods. Values obtained from basal and presumed flight rates of metabolism provide apparently the best current available estimates for migrating Palm Warblers.

LITERATURE CITED

BULLIS, H. R., JR. 1954. Trans-Gulf migration, spring 1952. Auk, **71**: 298–305.

CALDWELL, L. D., E. P. ODUM, AND S. G. MARSHALL. 1963. Comparison of fat levels in migrating birds killed at a central Michigan and a Florida Gulf coast television tower. Wilson Bull., **75**: 428–434.

JOHNSTON, D. W. 1962. Lipid deposition and gonadal recrudescence in response to photoperiodic manipulations in the Slate-colored Junco. Auk, **79**: 387–398.

JOHNSTON, D. W. 1965. Ecology of the Indigo Bunting in Florida. Quart. J. Florida Acad. Sci., **28**: 199–211.

JOHNSTON, D. W., AND T. P. HAINES. 1957. Analysis of mass bird mortality in October, 1954. Auk, **74**: 447–458.

JOHNSTON, D. W., AND R. W. MCFARLANE. 1967. Migration and bioenergetics of flight in the Pacific Golden Plover. Condor, **69**: 156–168.

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. 2 (A. J. Marshall, ed.). New York, Academic Press.

KURODA, N. 1964. Analysis of variation by sex, age, and season of body weight, fat and some body parts in the Dusky Thrush, wintering in Japan: a preliminary study. Misc. Rep. Yamashina's Inst. Ornith. and Zool., **4**: 91–105.

LASIEWSKI, R. C. 1963. Oxygen consumption of torpid, resting, active, and flying hummingbirds. Physiol. Zool., **36**: 122–140.

LEFEBVRE, E. A. 1964. The use of D_2O^{18} for measuring energy metabolism in *Columba livia* at rest and in flight. Auk, **81**: 403–416.

MURRAY, B. G., JR., AND J. R. JEHL, JR. 1964. Weights of autumn migrants from coastal New Jersey. Bird-Banding, **35**: 253–263.

NISBET, I. C. T., W. H. DRURY, JR., AND J. BAIRD. 1963. Weight-loss during migration. Bird-Banding, **34**: 107–159.

ODUM, E. P. 1960. Lipid deposition in nocturnal migrant birds. Proc. XII Intern. Ornith. Congr., Helsinki 1958. Pp. 563–576.

ODUM, E. P. 1965. Adipose tissue in migratory birds. Chap. 6 *in* Handbook of Physiology, Amer. Physiol. Soc., Washington, D. C.

ODUM, E. P., D. T. ROGERS, AND D. L. HICKS. 1964. Homeostasis of the nonfat components of migrating birds. Science, **143**(3610): 1037–1039.

ROGERS, D. T., JR., AND E. P. ODUM. 1964. Effect of age, sex, and level of fat deposition on major body components in some wood warblers. Auk, **81**: 505–513.

STEVENSON, H. M. 1957. The relative magnitude of the trans-Gulf and circum-Gulf spring migration. Wilson Bull., **69**: 39–77.

TUCKER, V. A. 1966. Oxygen consumption of a flying bird. Science, **154**: 150–151.

YAPP, W. B. 1956. Two physiological considerations in bird migration. Wilson Bull., **68**: 312–319.

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