NEW ESTIMATES OF WEIGHT LOSS IN BIRDS DURING NOCTURNAL MIGRATION[1]

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ABSTRACT.—Weight loss during flight was estimated for 10 species of passerines of body weight 8–32 g, using a refinement of the method described by Hussell (1969). Analysis of 2,226 migrants, weighed after they were attracted to the Long Point lighthouse, Ontario during nocturnal flight, yielded a mean weight loss of 0.70% of body weight/h. Excluding the Blackpoll Warbler, which had a substantially lower rate of weight loss than any other species, mean weight loss was 0.91% of body weight/h. In this reduced group of 9 species, weight loss averaged about 62% of the rate of fat utilization predicted by Berger and Hart's (1974) flight metabolism data. *Received 18 December 1978, accepted 1 February 1980.*

FEW satisfactory estimates of weight loss or energy metabolism have been made for birds in migratory flight. Six estimates, which depend on measurements of weight or fat content of migrating birds at two geographic locations (Dolnik et al. 1963, cited in Hart and Berger 1972; Dolnik and Blyumental 1967) or on change in weight of birds passing a fixed point in the migratory path (Hussell 1969), show good agreement with physiological measurements of flight metabolism (Hart and Berger 1972).

In an earlier paper, a method for determining weight loss of birds during migratory flight was described (Hussell 1969). Veeries and Ovenbirds (see Table 2 for scientific names) were estimated to have lost 1.3 and 1.0% of body weight/h, respectively. Elsewhere, adult and immature Yellow-rumped (Myrtle) Warblers were estimated to have lost 1.0 and 1.2% of body weight/h, respectively (Hussell and Caldwell 1972). In this paper we describe refinements to the method and provide estimates of weight loss for seven additional species as well as improved estimates for Veery, Yellow-rumped Warbler, and Ovenbird.

The method used here for estimating weight loss depends on taking a series of samples of migrants as they arrive at the lighthouse at Long Point, Ontario during nocturnal migratory flight. The rate of change in mean weight of birds taken at different times during the night will be the same as the mean rate of weight loss of individual birds in flight, provided that birds taken at different hours are random samples drawn from the same population as characterized by weight at and time of flight initiation (Hussell 1969).

In the previous analysis, weight loss was estimated as the slope of a simple linear regression of weight on arrival time at the lighthouse for birds taken during a single night. Here, we introduce the concept of combining samples of the same species taken on different nights as groups within the regression. This procedure increases the sample size and gives a more precise estimate of mean weight loss, if the rates of weight loss on different nights are approximately the same. Age and sex classes may be grouped in a similar manner as samples from different nights. Another refinement in the present analysis is the addition of wing-chord length as an independent variable in the regression. In most species, weight is positively correlated

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[1] A contribution of the Long Point Bird Observatory.

The Auk 97: 547–558. July 1980

TABLE 1. Weight loss of birds in holding boxes.

Species	Hours held (range)	n	Mean weight[a] (g)	Weight loss (g/h)	Correction factor[b] (g/h)	Maximum applied correction[c] (g)
Swainson's Thrush	9.4–11.8	9	29.4	0.178	0.200	0.342
Grey-cheeked Thrush[d]	10.3–11.8	18	33.3	0.209	—	—
Veery	8.5–11.0	38	30.8	0.207	0.200	0.316
Yellow-rumped Warbler	6.3–7.0	14	13.2	0.152	0.145	0.429
Blackpoll Warbler	4.7–6.3	6	13.2	0.154	0.145	0.180
Ovenbird	8.9–11.6	3	19.1	0.140	0.170	0.248
White-throated Sparrow	6.3	4	26.3	0.123	0.190	0.222
Red-eyed Vireo	—	—	—	—	0.165	0.151
Common Yellowthroat	—	—	—	—	0.140	0.064
American Redstart	—	—	—	—	0.125	0.064
White-crowned Sparrow	—	—	—	—	0.190	0.383

[a] Mean weight of the individuals used to determine weight loss in holding boxes.

[b] Correction factor was calculated from the regression (see text) by substituting mean weights of all birds in the samples from Table 3.

[c] Maximum correction applied to the measured weights for each species.

[d] *Catharus minimus*.

with wing-chord length, so its inclusion as a variable in a multiple regression accounts for a portion of the variation in weight, thus allowing a more precise estimate of the relation between weight and time.

METHODS

The Long Point Lighthouse and the manner in which birds are attracted to it are described in Hussell (1969). Samples of birds were obtained on various nights from 1965 to 1972. Samples of fewer than 10 birds and those taken entirely within a period of 2 h or less on any one night were excluded from the analysis, as were species samples totalling fewer than 50 birds for all nights combined.

Field procedures were designed to determine weights of individual birds on arrival at the lighthouse and to estimate arrival times as accurately as possible. Live birds were picked up from the window ledges and gallery of the lighthouse as they arrived or at recorded intervals during the night. All birds of the selected species were taken and held in darkened boxes until they were processed. As soon as possible after capture they were either banded, weighed, measured, and released or taken as specimens for body component analysis (to be described elsewhere). Birds killed when they struck the lighthouse provided additional specimens, which were picked up when they fell or at recorded intervals during the night. The banded birds were weighed to the nearest 0.1 g, the wing-chord length was measured, and the time of weighing recorded. During autumn migration, banded birds were usually aged by skull pneumatization ("ossification") as HY (Hatching Year—hatched during the preceding summer) or AHY (After Hatching Year—older birds). Some species were sexed and/or aged by plumage characteristics. Time of death was recorded for specimens that had been captured live. All specimens were stored in plastic bags and frozen within 8 h. Weights (assumed to be the same as at death) and measurements of specimens were taken as for live birds, usually within 2 h of death but sometimes from the frozen specimens up to 10 days later. Autumn specimens were aged by skull ossification, and all specimens were sexed by dissection by L. D. Caldwell or his students at Central Michigan University, Mount Pleasant.

Arrival times were known exactly for birds captured as they arrived or picked up as they were killed. Other birds were collected live or picked up dead after known intervals, which were usually less than 1 h (but occasionally as much as 3.5 h), and were assumed to have arrived at the mean time of the preceding interval. In the case of the first collection of the night, the start of the preceding interval was estimated as the time when birds were first observed flying in the lighthouse beams.

Although live birds were weighed or taken as specimens as soon as possible after capture, it was necessary to apply corrections to the weights to compensate for weight loss between estimated time of arrival and time of weighing or death. The best estimate of this loss is provided by the mean rates of weight loss of seven species captured at the lighthouse during the main procedure and held for several hours in individual darkened boxes (Table 1). A weighted linear regression (with weighting factors equal to the sample sizes) of $\log R$ on $\log W$, where R is the mean rate of weight loss in g/h and W is the mean weight in g for each species sample, yielded the relationship: $\log R = 0.347 \log W - 1.221$. Correction factors for rate of weight loss in captivity were calculated for each of the 10 species sampled by substituting the mean weight of all birds in the sample for W in the equation (Table 1). The weight correction for each individual was calculated as the correction factor for that species multiplied by the time between arrival and weighing or death, and was added to the measured weight. Applied corrections were never more than 0.43 g (Table 1).

Weight loss during migration was determined by the combination of stepwise and hierarchical multivariate regressions, using the SPSS (Statistical Package for the Social Sciences) program "Multiple Regression" at the University of Guelph Computing Center, Ontario. The corrected weight, Y, was always the dependent variable, and the arrival time, X_1, and wing-chord length, X_2, were included as independent variables in all regressions, because the objective of the analysis was to find the best relationship between Y and X_1, taking into account the effects of X_2. An analysis of variance attributable to age, sex, and sample (night) was performed by creating "dummy" variables within the SPSS program for each of these categorical factors and for the interaction of sample with time, age, and sex, and the interaction of age and sex with each other and with both time and wing chord. It was assumed that there was no interaction between sample and wing chord. In the one species for which we have both spring and autumn samples (Swainson's Thrush), variance attributable to interaction of season and time was also examined.

Samples from different nights often differed significantly in adjusted mean weights. Such differences are to be expected, because (1) average take-off weights are likely to differ between nights due to seasonal and local factors affecting fat deposition, and (2) average time of flight initiation presumably changes with date in parallel with the time of sunset. Therefore, variables for sample (night) were always included in regressions combining data for different nights, regardless of whether or not their coefficients were statistically significant. Age and sex variables (if any) were next made available for stepwise inclusion in the regressions if their effects were significant at the 5% level. Interaction terms between the categorical factors (age, sex, sample) were then made available, and, finally, terms for interaction between categorical factors and time and wing chord were made available for inclusion in the regression. Thus it was assumed that it was more probable that there was a difference in mean weight (adjusted for time and wing chord) between samples, or age or sex groups, than that there was a difference in the rate of change of weight with time and wing chord between such groups. The latter (interaction) variables were brought into the regression only if their effects remained significant after the former (additive) effects had been taken into account.

The procedure will be illustrated with three increasingly complex examples.

For a single sample of birds captured on one night (with no age or sex determinations) the regression takes the form:

$$Y = a + b_1X_1 + b_2X_2,$$

where a is a constant and b_1 and b_2 are the partial regression coefficients of weight on time and wing chord, respectively. b_1 is the best estimate of rate of weight change during migration and is negative if the birds are losing weight.

If two samples are available (for two different nights), then the regression has the form:

$$Y = a_1 + a_2N_2 + b_1X_1 + b_2X_2,$$

where N_2 is a dummy variable, which equals 0 for the first sample and 1 for the second sample, a_2 is the difference between the adjusted means for the two nights, and b_1 and b_2 are estimates of rates of change in weight with time and wing length, respectively, for the pooled data for the two nights. It should be noted that a dummy variable for sample 1 is not required, as the conditions for that group are met when $N_2 = 0$. The procedure can be extended to three or more nights by including additional dummy variables in the regression (N_3, N_4, etc.)

To investigate the possibility that rate of weight change differs between nights, an interaction term for sample and time is included in the regression; thus:

$$Y = a_1 + a_2N_2 + b_1X_1 + b_{12}(N_2X_1) + b_2X_2,$$

where (N_2X_1) is a dummy variable created by multiplying N_2 by X_1 for each case, and b_{12} is the difference in rate of weight change with time between sample 2 and sample 1. Again, this procedure can be extended to additional samples by creating additional interaction variables (N_3X_1, N_4X_1, etc.)

Additive effects of age and sex and their interactions with time and wing length can be examined in a similar manner by creating additional dummy variables. In general, variables used in the stepwise procedure were excluded from the regression unless their coefficients were significant at the 5% level after all variables with higher significance levels had already been brought into the regression. Factors examined in each species are described in the results section.

The relation between rate of weight loss in flight, L_w, and mean body weight, W, of each species was determined from a linear regression of the transformed estimates of weight loss on body weight in the form: $\log L_w = \log a + b \log W$.

RESULTS

WEIGHT LOSS DETERMINATIONS

Procedures for determining weight loss are given in the species accounts below. Samples are described in this sequence: sample number, date, number of individuals (n), and number in each age and sex category. Birds of unknown age or sex that were not used in the final weight-loss determinations have been excluded. Sex breakdown is given only when complete samples were sexed. Age and sex codes are: HY—hatching year, SY—second year, AHY—after hatching year, ASY—after second year, U—unknown age, M—male, F—female. Results of regression analyses are shown in Table 2.

Swainson's Thrush.—Samples taken on 8 nights totalled 241 birds: #1, 6–7 May 1965, $n = 15$; #2, 1–2 June 1965, $n = 14$; #3, 18–19 May 1966, $n = 14$; #4, 24–25 May 1971, $n = 27$; #5, 16–17 May 1972, $n = 11$; #6, 12–13 September 1971, $n = 57$ (44 HY, 13 AHY); #7, 13–14 September 1971, $n = 36$ (27 HY, 9 AHY); #8, 12–13 September 1972, $n = 67$ (46 HY, 21 AHY).

This is the only species for which we have both spring and autumn samples. Among the spring samples, only sample 1 showed a significant weight loss, and the pooled sample of 81 birds gave a rate of weight loss of 0.461 g/h, which is also significantly different from zero ($P < 0.05$).

Age (HY vs. AHY) was included in the regressions for autumn samples, because the pooled samples showed a significant age effect. All three samples showed a significant increase of weight with wing length, as did the pooled autumn sample of 160 birds, but there were no significant changes of weight with time.

As there were no interactions between season or sample and time, a pooled estimate of weight change with time and wing length for all nights in both seasons was obtained by including sample and age in the regression (all spring birds were AHY). This gave a weight loss estimate of 0.232 g/h (not significant).

Veery.—Samples taken on 7 nights totalled 392 birds: #1, 6–7 May 1965, $n = 76$; #2, 11–12 May 1966, $n = 37$; #3, 18–19 May 1966, $n = 37$; #4, 17–18 May 1968, $n = 111$; #5, 13–14 May 1969, $n = 64$; #6, 24–25 May 1971, $n = 27$; #7, 16–17 May 1972, $n = 40$.

Sample 1 is the same as reported in Hussell (1969) except that four birds have been removed because wing measurements were not available. A separate analysis of 70 sexed specimens (46 males and 24 females) from samples 4 and 5 showed that the adjusted mean weights of males were about 2.6 g heavier and significantly greater than those of females. As the remaining 322 birds in the total sample were not sexed, it is not practical to use sex as a factor in the full analysis. Provided that males and females are randomly distributed with respect to time, sex differences should have little effect on the estimated weight loss from the pooled data, and the large size of this sample increases our confidence in this assessment.

Three of the seven samples had a significant weight loss, while five showed a significant positive relationship between weight and wing length. The weight increase with time in sample 7 was not significantly different from zero but was significantly different from the rate of weight change with time of the other six samples after the additive effects of different sample groups were included.

The statistical evidence indicates, therefore, that sample 7 should not be pooled with the other samples, and, because it is a small sample, it would appear that the most satisfactory estimate of weight loss would come from combining samples 1–6. Mean weight loss for samples 1–6 is then 0.362 g/h, which is significantly different from zero ($P < 0.01$).

There are several arguments, however, against excluding sample 7. First, the anomalous result in sample 7 may be due to a nonuniform distribution of males and females in relation to time within this small sample (females early in the night, males late in the night; see above). Exclusion of sample 7 might tend to bias the pooled result in the opposite direction (note the extraordinarily high estimate of weight loss in sample 3, another small sample). An additional consideration is that real differences in rates of weight loss may occur between nights due to different weather conditions or different mean weights of birds (heavier birds should have higher flight metabolism and weight loss). Furthermore, varying deviations from the assumptions of the model on different nights may result in apparent differences in estimated rates of weight loss. In addition, about 5% of the samples should show chance variations of the magnitude found in sample 7, even if there are no real differences between samples. This was one of only two samples that showed a statistically significant difference in rates of weight change between nights within the same species (the other was Yellow-rumped Warbler, sample 3). Given the possibility that the difference may be due to chance or to nonrandom distribution of sexes within a small sample, and because our objective is to obtain the best estimate of mean weight loss in each species under average conditions, we believe that excluding this sample from the pooled estimate may introduce an undesirable bias in the result. The pooled data from samples 1–7 yielded a significant weight loss of 0.271 g/h, substantially lower than the 0.41 g/h reported by Hussell (1969).

Red-eyed Vireo.—Samples taken on 2 nights totalled 63 birds: #1, 24–25 May 1970, $n = 53$ (23M, 30F); #2, 24–25 May 1971, $n = 10$.

In sample 1 adjusted mean weights of males were 1.36 g heavier than of females ($P < 0.01$). In view of this sex difference and because sample 2 was unsexed and consisted of only 10 birds, we excluded it from our estimate of weight loss for the species. Although the rate of weight change of females in sample 1 (−0.385 g/h) was significantly different than of males (+0.120 g/h) after the additive effect of sex was taken into account ($P < 0.01$), we pooled the sexes to obtain our best estimate of weight loss for the species, 0.137 g/h, which is not significantly different from zero.

Yellow-rumped (Myrtle) Warbler.—Samples taken on 8 nights totalled 705 birds: #1, 16–17 October 1966, $n = 52$ (33 HY, 19 AHY); #2, 11–12 October 1967, $n = 69$; #3, 3–4 October 1969, $n = 20$ (15 HY, 5 AHY); #4, 11–12 October 1969, $n = 424$ (158 HY, 266 AHY); #5, 12–13 October 1969, $n = 43$, (16 HY, 27 AHY); #6, 16–17 October 1969, $n = 50$ (32 HY, 18 AHY); #7, 31 October–1 November 1970, $n = 14$ (11 HY, 3 AHY); #8, 6–7 October 1972, $n = 33$ (21 HY, 12 AHY).

The largest sample (# 4) is the one previously reported by Hussell and Caldwell (1972). It had a significant weight loss when considered alone, while four of the eight samples showed a significant positive relationship between weight and wing chord. In two samples (# 4 and 5), HY birds were significantly heavier, so sample 2 (which was unaged) was excluded from the pooled estimates. A separate analysis

TABLE 2. Group and pooled regression coefficients for change in weight with time and wing chord.

Species and season	Sample number(s)	*n*	Regression coefficients for:				Other variables in regression[b]
			Time[a] (g/h)		Wing chord[a] (g/mm)		
			b	s_b	*b*	s_b	
Swainson's Thrush (*Catharus ustulatus*) Spring	1	15	−0.850*	±0.329	0.672	±0.351	
	2	14	0.232	±2.005	−0.263	±0.406	
	3	14	−0.422	±0.561	0.353	±0.243	
	4	27	−0.144	±0.340	0.133	±0.193	
	5	11	−0.273	±0.620	0.641	±0.602	
	1–5	81	−0.461*	±0.209	0.176	±0.129	
Autumn	6	57	0.167	±0.218	0.340**	±0.102	HY
	7	36	−0.371	±0.294	0.347*	±0.164	HY
	8	67	0.142	±0.444	0.290*	±0.112	HY
	6–8	160	−0.023	±0.160	0.345**	±0.066	HY**
Spring and autumn	1–8	241	−0.232	±0.126	0.292**	±0.060	HY*
Veery (*Catharus fuscescens*) Spring	1	76	−0.379**	±0.129	0.496**	±0.093	
	2	37	−0.031	±0.212	0.033	±0.128	
	3	37	−0.957**	±0.275	0.772**	±0.148	
	4	111	−0.317**	±0.188	0.479**	±0.067	
	5	64	−0.370	±0.268	0.441**	±0.092	
	6	27	−0.489	±0.281	0.234	±0.133	
	7	40	0.182	±0.198	0.287**	±0.091	
	1–7	392	−0.271**	±0.079	0.378**	±0.037	
Red-eyed Vireo (*Vireo olivaceus*) Spring	1	53	−0.137	±0.089	0.163	±0.103	M**
	2	10	0.048	±0.410	0.075	±0.269	
Yellow-rumped (Myrtle) Warbler (*Dendroica coronata coronata*) Autumn	1	52	−0.072	±0.074	0.120*	±0.057	HY
	2	69	−0.181	±0.096	0.046	±0.036	
	3	20	0.446	±0.217	0.078	±0.088	HY
	4	424	−0.145**	±0.028	0.169**	±0.015	HY**
	5	43	−0.146	±0.085	0.110	±0.056	HY**
	6	50	−0.065	±0.076	0.138*	±0.059	HY
	7	14	0.181	±0.346	0.093	±0.100	HY
	8	33	−0.089	±0.286	0.206*	±0.091	HY
	1, 3–8	636	−0.124**	±0.023	0.157**	±0.014	HY**, HY-N_5**
Blackpoll Warbler (*Dendroica striata*) Autumn	1	33	−0.099	±0.073	0.287**	±0.059	
	2	181	0.002	±0.039	0.100**	±0.022	
	1–2	214	−0.008	±0.035	0.116**	±0.021	
Common Yellowthroat (*Geothlypis trichas*) Spring	1	139	−0.158**	±0.028	0.125**	±0.030	M**
American Redstart (*Setophaga ruticilla*) Spring	1	76	−0.134**	±0.033	0.171**	±0.025	
Ovenbird (*Seiurus aurocapillus*) Autumn	1	17	−0.561*	±0.255	0.190	±0.097	
	2	88	−0.191**	±0.043	0.073	±0.055	
	3	11	0.114	±0.475	−0.023	±0.186	
	1–3	116	−0.196**	±0.040	0.092	±0.047	
White-crowned Sparrow (*Zonotrichia leucophrys*) Autumn	1	68	−0.091	±0.113	0.550**	±0.081	

TABLE 2. Continued.

Species and season	Sample number(s)	n	Regression coefficients for:				Other variables in regression[b]
			Time[a] (g/h)		Wing chord[a] (g/mm)		
			b	s_b	b	s_b	
White-throated Sparrow	1	27	−0.299*	±0.108	0.469**	±0.145	
(*Zonotrichia albicollis*)	2	39	−0.524	±0.312	0.689**	±0.133	
Spring	3	51	−0.154	±0.207	0.404**	±0.098	
	4	19	−0.713	±1.173	0.501*	±0.181	
	5	101	−0.389**	±0.138	0.393**	±0.079	
	6	54	−0.932*	±0.390	0.418**	±0.107	
	1–6	291	−0.343**	±0.080	0.443**	±0.045	

[a] The figures given are the partial regression coefficient b and its standard error s_b. One and two asterisks (* and **) indicate coefficients significantly different from zero at the 5% and 1% levels, respectively.

[b] Factors included as dummy variables in the regression (see text). Age: HY (reference age: AHY); sex: M (reference sex: F); age-sample interaction: HY-N_5. Significance levels are indicated by asterisks in the same way as for the regression coefficients (footnote a). Sample variables (N_1, N_2, etc.) are not shown in the table but are included for all samples (except reference sample) in all regessions that pool data from more than one sample. For example, in the pooled regression for samples 1–7 in the Veery, sample 1 was the reference sample, and the regression included sample variables N_2, N_3, N_4, N_5, N_6, N_7.

of 140 sexed birds from samples 3, 4, and 5 showed no effect of sex after age differences had been included. When all samples (except # 2) were combined, age had a significant effect on mean weight, the HY birds being heavier as in samples 4 and 5. Interaction of sample group with age was also investigated, and variable HY-N_5 was included in the final pooled regression, because HY birds on that night were significantly heavier than on other nights. Rate of weight change in sample 3 (20 birds) was positive and significantly different from the others, but it was included in the pooled estimate for the same reasons advanced for Veery sample 7 (see above). The pooled weight loss estimate was 0.124 g/h; both it and the wing-chord coefficient were significant.

Blackpoll Warbler.—Samples taken on 2 nights totalled 214 birds: #1, 28–29 September 1965, $n = 33$ (2 HY, 1 AHY, 30 U); #2, 8–9 September 1970, $n = 181$ (75 HY, 103 AHY, 3 U).

A separate analysis of 93 sexed and aged specimens from sample 2 showed no effect of sex or age, and there was no significant effect of age in the total sample 2. Thus we are justified in excluding age from the analysis and in using sample 1, in which most birds were of unknown age. Neither of the samples showed a significant weight loss. The pooled data gave a small nonsignificant loss in weight with time and a significant positive wing-chord coefficient.

Common Yellowthroat.—One sample only: #1, 24–25 May 1970, $n = 139$ (74 M, 65 F).

Males were significantly heavier after adjusting for time and wing length (mean difference 0.92 g), but sex had no effect on the time and wing length coefficients. There was a significant rate of weight loss of 0.158 g/h, and the wing-chord coefficient was positive and significant.

American Redstart.—One sample only: #1, 24–25 May 1970, $n = 76$ (11 ASY/M, 21 SY/M, 44 AHY/F).

TABLE 3. Estimates of weight loss during nocturnal migratory flight for 10 species.

		Rate of weight change (g/h)		Mean body weight[b] (g)	Mean rate of weight change (% body weight/h)
Species	n	Mean[a]	95% confidence interval		
Swainson's Thrush	241	−0.232	−0.481–+0.017	31.81	−0.73
Veery	392	−0.271**	−0.427–−0.114	32.28	−0.84
Red-eyed Vireo	53	−0.137	−0.309–+0.035	17.68	−0.77
Yellow-rumped Warbler	636	−0.124**	−0.170–−0.076	12.94	−0.96
Blackpoll Warbler	214	−0.008	−0.077–+0.061	12.70	−0.06
Common Yellowthroat	139	−0.158**	−0.214–−0.103	11.20	−1.41
American Redstart	76	−0.134**	−0.199–−0.068	8.18	−1.64
Ovenbird	116	−0.196**	−0.276–−0.116	19.52	−1.00
White-crowned Sparrow	68	−0.091	−0.317–+0.135	27.95	−0.33
White-throated Sparrow	291	−0.343**	−0.499–−0.186	26.49	−1.29

[a] Two asterisks (**) indicate that the rate of weight change is significantly different from zero at the 1% level. (Others not significant, $P > 0.05$.)

[b] Mean body weight of the entire sample used to determine weight change.

There were no significant effects of age or sex. Rate of weight loss was significant at 0.134 g/h, and the wing-chord coefficient was positive and significant.

Ovenbird.—Samples taken on 3 nights totalled 116 birds: #1, 2–3 September 1966, $n = 17$ (12 HY, 5 AHY); #2, 21–22 September 1966, $n = 88$ (22 HY, 65 AHY, 1 U); #3, 13–14 September 1971, $n = 11$ (3 HY, 8 AHY).

Sample 2 is the same as in Hussell (1969), with 8 birds removed because wing-chord measurements were not available. No age effects were detected in these samples, and the pooled weight-loss estimate of 0.196 g/h is significant and similar to the one in Hussell (1969). There was no significant relationship between weight and wing chord ($0.10 > P > 0.05$).

White-crowned Sparrow.—One sample only: #1, 12–13 October 1969, $n = 68$ (42 HY, 26 AHY).

No age effect was detected, and the sample yielded a nonsignificant weight loss (0.091 g/h) and a significant positive wing-chord coefficient.

White-throated Sparrow.—Samples taken on 6 nights totalled 291 birds: #1, 26–27 April 1965, $n = 27$; #2, 11–12 May 1966, $n = 39$; #3, 30 April–1 May 1967, $n = 51$: #4, 7–8 May 1969, $n = 19$; #5, 27–28 April 1970, $n = 101$; #6, 28–29 April 1970, $n = 54$.

Three of the six sample groups had a significant weight loss with time, and the pooled data gave a significant rate of loss of 0.343 g/h. All six groups and the pooled data showed a significant positive wing-chord coefficient.

RELATIONSHIP BETWEEN WEIGHT LOSS AND BODY WEIGHT.

Rates of weight loss during nocturnal migratory flight are summarized for 10 species in Table 3. The estimates vary in their reliability as indicated by the 95% confidence intervals. Mean weights of the species involved range from 8 to 32 g, and weight-loss estimates for six species whose weight losses were significantly greater than zero ranged from 0.84 to 1.64% of body weight/h and averaged 1.19% of body weight/h. Excluding nonsignificant estimates from the average introduces a bias, however, as high estimates are more likely to be significantly different from zero than low ones. If we include all 10 values, the mean rate of weight loss is 0.90% of body weight/h. Because the relation between weight loss and body weight

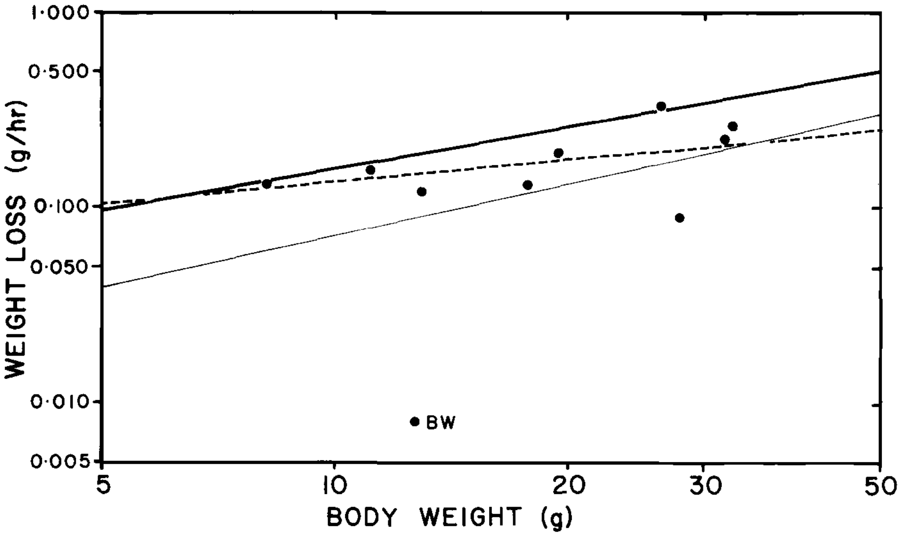

Fig. 1. Logarithmic plot of weight loss during nocturnal migration in relation to body weight for 10 species of passerine birds. The heavy line is Berger and Hart's (1974) equation for flight metabolism converted to fat loss (see text): $L_f = 0.0304W^{0.72}$. The narrow line is a regression fitted to all 10 data points: $L_w = 0.0093W^{0.90}$. The broken line is a regression fitted to the data excluding the point for the Blackpoll Warbler (BW): $L_w = 0.0533W^{0.40}$.

is not linear, a better estimate of average weight loss can be derived from the logarithmically transformed data. A logarithmic plot of weight loss, L_w, against body weight, W, is shown in Fig. 1. The regression gives the relationship $L_w = 0.0093W^{0.90}$, where L_w is rate of weight loss in g/h and W is body weight in g. The mean rate of weight loss is 0.127 g/h for a hypothetical bird of 18.2 g, which represents 0.70% of body weight/h. If we exclude the estimate for the Blackpoll Warbler, which is much lower than for any other species, the equation becomes $L_w = 0.0533W^{0.40}$, and the mean rate of weight loss becomes 0.173 g/h or 0.91% of body weight/h for an 18.9-g bird.

DISCUSSION

Estimates of weight loss of birds during migratory flight have been reviewed extensively elsewhere (e.g. Nisbet 1963, Raveling and LeFebvre 1967, Hussell 1969, Hart and Berger 1972, Berger and Hart 1974, Alerstam 1979) and will not be enumerated again here. Hart and Berger (1972) considered that only the estimates of Dolnik and Blyumental (1967) and Hussell (1969) have adequate statistical reliability. Most weight-loss estimates for small passerines are of the order of 1% of body weight/h. Those of Dolnik and Blyumental (1967) and more recent estimates reported by Dolnik and Gavrilov (1973) for four passerines of weight 12.5–39.5 g are of the order of 3% of body weight/h. There appears to be no good explanation for this discrepancy, although higher weight loss is possibly characteristic of relatively short-distance migrants (Alerstam 1979).

Our new estimates of weight loss (regardless of whether we take 0.70% or 0.91% of body weight/h as the best mean value; see discussion below) are towards the lower end of the range of all previously reported estimates and are lower than the average values reported from an earlier version of the same method (Hussell 1969, Hussell and Caldwell 1972). The differences are attributable to larger sample sizes and improved methodology.

Weight loss is a crude measure of the outcome of several physiological processes that a bird undergoes during flight. In the present state of the art, estimates of weight loss of birds in migratory flight are valuable, because they must be capable of reconciliation with what is known about physiological processes that cannot be monitored easily in free-flying wild birds. Their interpretation, however, is problematical (Hussell 1969, Hart and Berger 1972, Berger and Hart 1974).

The body weight of a bird can be regarded as consisting of three components: fat, water, and a dry lean component. If the nonfat components remain constant during nocturnal migratory flight (Odum et al. 1964), weight loss will represent the fat used as fuel to provide energy for flight. Although there are reasons for believing that water content is not strictly constant in flight (Berger and Hart 1974), we will assume that weight loss is equal to change in fat content for the purpose of evaluating our weight-loss estimates in relation to measurements of flight metabolism (Hussell 1969). To do so, oxygen consumption and energy expenditure in flight are calculated from fat (i.e. weight) loss, and vice versa, using 9.5 Kcal/g fat and 0.21 l O_2/Kcal as conversion factors.

Berger and Hart (1974) showed that oxygen consumption of birds in flight $\dot{V}_{O_2}$ (ml O_2/min) is related to body weight in g by the equation $\dot{V}_{O_2} = 1.01W^{0.72}$. Included in their regression were 8 direct measurements of $\dot{V}_{O_2}$, 2 measurements derived from fat loss and carbon dioxide production using the D_2O^{18} method, and 1 calculated from fat loss of diurnally migrating birds. Body weight of the 11 species was 3–1,020 g. Converting to fat loss, L_f, in g/h, their equation becomes $L_f = 0.0304W^{0.72}$. This relationship is compared with our results in Fig. 1.

All except one of our weight-loss estimates are less than the fat loss predicted by Berger and Hart's equation. The regression fitted to our data gives a weight loss for an 18.2-g bird of approximately 52% of fat loss derived from Berger and Hart's equation. Excluding the Blackpoll Warbler, weight loss is approximately 68% of predicted fat loss for an 18.9-g bird.

Regressions fitted to our data show that weight loss is proportional to the 0.90 power of body weight, or to the 0.40 power of body weight if the Blackpoll Warbler is excluded. Flight metabolic rate and fat loss are proportional to the 0.72 power of body weight (see above). Because our data are for a relatively narrow range of body weights (8–33 g), the relation between weight loss and the power of body weight cannot be determined as precisely as would be possible if we also had weight-loss estimates for some much larger birds.

We attempted to test whether or not our weight-loss regression ($L_w = 0.0093W^{0.90}$) is significantly different from the regression fitted to the data published by Berger and Hart (1974), but we found that the variances about the regressions are not homogeneous ($P < 0.01$). If we remove the Blackpoll Warbler from our data, there is no significant difference between the variances or between the slopes of the regressions. The adjusted means of the two sets of data are significantly different, however, with weight loss estimated at 62.2% of the fat loss predicted by the Berger and Hart data. If we use this covariance model, the equation for weight loss (excluding the Blackpoll Warbler) becomes $L_w = 0.0217W^{0.71}$, and for fat loss the equation is $L_f = 0.0349W^{0.71}$, which is close to the relationship derived from the Berger and Hart data alone.

If we assume that our results are not biased toward conservative weight loss estimates, the difference from the Berger and Hart relationship could be due to (1) a lower energy use by birds in nocturnal migratory flight than by birds under the experimental conditions used in determining Berger and Hart's equation, or (2) an increase in the nonfat components of body weight (primarily retention of metabolic water). It is impossible to distinguish between these two alternatives with the present evidence, but a preliminary analysis indicates that fat loss was the only significant component of weight loss among specimens from Yellow-rumped Warbler sample 4 (Hussell and Caldwell 1972). Thus a lower energy expenditure under conditions of migratory flight appears to be a reasonable possibility, at least in that species.

The Blackpoll Warbler gave the lowest estimate of weight loss of any species (0.008 ± 0.035 g/h). The estimate was derived from samples of 33 and 181 birds on the nights 28–29 September 1965 and 8–9 September 1970. The larger sample was the only single-night sample of more than 75 birds in any species that did not show a significant weight loss, even though the standard error of the determination is well within the range of other samples. Furthermore, the upper limit of the confidence interval for the Blackpoll Warbler yields a weight loss of only 0.61% of body weight/h and barely overlaps the lower confidence limit of 0.60% of body weight/h for the Yellow-rumped Warbler, a species that is very similar in weight, wing length, and build to the Blackpoll Warbler. Inclusion of the point for the Blackpoll Warbler gives a relation between weight loss and body weight that appears to be a relatively poor fit to the majority of the other data points (Fig. 1). To estimate energy utilization in nocturnal migratory flight, therefore, we believe that the covariance equation derived from all species except the Blackpoll Warbler and an average value of 0.91% loss of body weight/h are more likely to be appropriate for most small passerines.

Thus it appears that the result for the Blackpoll Warbler is anomalous. This may be due to a breakdown of the assumptions of the model for the two Blackpoll Warbler samples, but the result should not be rejected out of hand in view of the possibility that the Blackpoll Warbler may be exceptionally well adapted for long distance flights (Nisbet et al. 1963, Alerstam 1979). Low energy utilization and/or high retention of metabolic water are likely to be advantageous for long flights and may contribute to the difference in weight loss between the Blackpoll Warbler and relatively short-distance migrants such as the Yellow-rumped Warbler. Such a conclusion is entirely speculative, however, until additional large samples of Blackpoll Warblers have been examined.

Our weight-loss estimates for most species show reasonably good agreement with predictions from experimental determinations of flight metabolism, indicating that the method described here is a useful way of monitoring changes in birds during migratory flight. Large samples must be used to obtain satisfactory estimates, and preferably they should be taken on several different nights to limit the effects of unusual conditions. Use of the procedure to determine change in body components of migrants will help to refine estimates of energy expenditure and will elucidate the significance of water loss in migratory flight. Results of such an analysis will be reported elsewhere (Hussell et al. in prep.).

ACKNOWLEDGMENTS

We are indebted to many people who participated in the field work at Long Point, and we particularly wish to thank the following who were directly involved in collecting the data on which this paper is based: M. Alexander, D. Baldwin, J. Bradshaw, M. S. W. Bradstreet, A. D. Brewer, M. Connolly, H.

Craw, T. Davis, J. Evans, B. Fearis, G. A. Harbour, C. Holdsworth, G. L. Holroyd, E. W. Keith, H. MacPherson, R. Montgomerie, G. W. Page, A. Salvadori, J. Strauch, E. Tull, R. Whittam, J. Woodford, and P. Woodford. Access to the Long Point Lighthouse was made possible through the kind permission of J. S. Barrick, District Marine Agent, Canadian Ministry of Transport, and the friendly cooperation of the lighthouse keepers, R. W. Ansley, W. Lamb, and C. Scofield, and their families was most helpful and appreciated. Much of the fieldwork would have been impossible without the aid of grants to the Long Point Bird Observatory from the Canadian National Sportsmen's Show and the Federation of Ontario Naturalists. Computer work and preparation of the paper were supported by a Wintario grant.

LITERATURE CITED

ALERSTAM, T. 1979. Wind as a selective agent in bird migration. Ornis Scandinavica 10: 76–93.

BERGER, M., & J. S. HART. 1974. Physiology and energetics of flight. Pp. 415–477 *In* Avian biology, vol. 4 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

DOLNIK, V. R., & V. I. BLYUMENTAL. 1967. Autumnal premigratory and migratory periods in the Chaffinch (*Fringilla coelebs coelebs*) and some other temperate zone passerine birds. Condor 69: 435–468.

———, & V. M. GAVRILOV. 1973. Energy metabolism during flight of some passerines. Pp. 288–296 *In* Bird migrations—ecological and physiological factors. New York, John Wiley and Sons.

HART, J. S., & M. BERGER. 1972. Energetics, water economy and temperature regulation during flight. Proc. 15th Intern. Ornithol. Congr.: 184–199.

HUSSELL, D. J. T. 1969. Weight loss of birds during nocturnal migration. Auk 86: 75–83.

———, & L. D. CALDWELL. 1972. Flight metabolism of the Myrtle Warbler (*Dendroica coronata*) during nocturnal migration (Abstract). Proc. 15th Intern. Ornithol. Congr.: 653–654.

NISBET, I. C. T. 1963. Weight-loss during migration, part 2: Review of other estimates. Bird-Banding 34: 139–159.

———, W. H. DRURY, JR., & J. BAIRD. 1963. Weight loss during migration, part 1: Deposition and consumption of fat by the Blackpoll Warbler *Dendroica striata*. Bird-Banding 34: 107–138.

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

RAVELING, D. G., & E. A. LEFEBVRE. 1967. Energy metabolism and theoretical flight range of birds. Bird-Banding 38: 97–113.