WEIGHT LOSS OF BIRDS DURING NOCTURNAL MIGRATION[1]

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Several attempts have been made to estimate energy metabolism of birds during migratory flight (Odum, 1960; Nisbet, 1963; Raveling and LeFebvre, 1967). Estimates of weight lost by migrants during flight are relevant to these studies because weight loss must be reconciled with related physiological processes, including energy utilization. In this paper I am concerned primarily with weight loss during migratory flight, the estimates being based on weights of Veeries (*Hylocichla fuscescens*) and Ovenbirds (*Seiurus aurocapillus*) attracted to the lighthouse at Long Point, Ontario during nocturnal migration.

Ideally we would like to be able to weigh an individual bird before and after a migratory flight of known duration to determine its weight loss. So far such direct measurements have not been achieved with wild birds, and other, indirect methods have been used to estimate weight loss. One method is to weigh samples of birds from what is believed to be the same population, before and after a migratory flight whose duration can be estimated (Helms, 1959; Nisbet et al., 1963). Another approach, the one used here, is to take a series of samples of migrants as they pass a fixed point on the migratory path, and to assume that differences between the mean weights of birds arriving at different times are the same as the mean weight changes of individual birds flying during the same time intervals. This method is based on that used by Graber and Graber (1962) to estimate weight loss during nocturnal flight of thrushes killed at a television tower in Illinois.

If samples of nocturnal migrants passing overhead at particular times are obtained from the lighthouse, the mean rate of weight loss between samples taken at different times on the same night represents the mean rate of weight loss of individuals during migratory flight, provided that the following assumptions are true: (1) birds trapped or killed at different times represent groups of migrants that started their flights at the same mean weight and at the same mean time; (2) time of trapping or kill represents arrival time at the lighthouse, or alternatively, weight loss during circling flight around the lighthouse is the same as during normal migratory flight; (3) the probability that a bird will be trapped or killed is independent of its weight; (4) the probability that a bird will end its flight does not depend on its weight, at least during the sampling period.

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

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Methods

The Long Point Lighthouse is situated at the eastern end of Long Point, a sandy peninsula extending some 20 miles into Lake Erie from near the middle of the north shore. The lighthouse is 102 feet high, the center of the light being 96 feet above ground level and about 100 feet above lake level. A series of rotating prisms concentrates the light from a 400-watt mercury vapor lamp into four beams that make a complete revolution every 32 seconds, producing one flash of light every 8 seconds. In clear weather the light can be seen at least as far away as Erie, Pennsylvania, about 29 miles distant on the south shore of the lake. Nocturnal migrants are attracted to the light mainly during overcast conditions with moderate to poor visibility. Birds then approach and circle the light, sometimes in large numbers, and some are killed when they hit the windows or other parts of the structure. Larger numbers of birds usually fly into the windows and flutter down to rest on the window ledges, gallery, or railings, where they remain for a considerable time and can readily be caught by hand.

Samples of Veeries and Ovenbirds were obtained on the nights of 6–7 May 1965 and 21–22 September 1966, respectively. Live birds were collected from the window ledges, etc., at intervals during the night, all birds present being taken. The birds were held in darkened boxes and as soon as possible after capture they were banded and weighed to the nearest 0.1 g, the wing chord was measured (from the bend to the tip of the folded, unflattened wing), and the time recorded. The Ovenbirds were also aged by skull ossification using the method described by Baird (in Norris, 1961). In this way the weights of most birds were obtained within a few minutes of capture, and few were held for more than an hour before being weighed. The birds were released immediately after processing. Dead birds were picked up at the base of the tower at intervals during the night and stored in plastic bags. The dead Veeries were weighed during the morning after the kill. The Ovenbirds were frozen on the morning after the kill, and the same data as for the live birds were obtained from them 10 days later.

In most cases the times of arrival of individual birds at the lighthouse were not known precisely. The live Veeries were taken from the lighthouse and dead birds were picked up at the base of the tower each hour starting at midnight, Eastern Standard Time. They were assumed to have arrived during the preceding hour, except for the first batch which was assumed to have arrived during the preceding 2 hours as the flight started at about 2200 hours. Thus mean arrival times for the groups of Veeries were at 2300, 0030, 0130, 0230, and 0330 hours. Arrival times of Ovenbirds were calculated in the same way. For the live Ovenbirds the arrival times are usually known more accurately (maximum error $\pm$ 0.5 hour) than for the Veeries, because one man was collecting the birds as they arrived during most of the night. The dead Ovenbirds were picked up at irregular intervals and possible errors in arrival times vary from $\pm$ 0.25 hour to $\pm$ 1.75 hours.

Although the live birds were weighed 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. The best available estimate of this loss is provided by the mean rate of weight loss of birds trapped at the lighthouse and held until morning in individual boxes. Mean weight losses of 23 Veeries and three Ovenbirds held overnight were 0.21 g/hr and 0.14 g/hr, respectively. The corrections actually applied to the measured weights varied from 0 to 0.3 g for the Veeries and 0 to 0.1 g for the Ovenbirds.

Statistical methods in this paper follow standard procedures described in Dixon

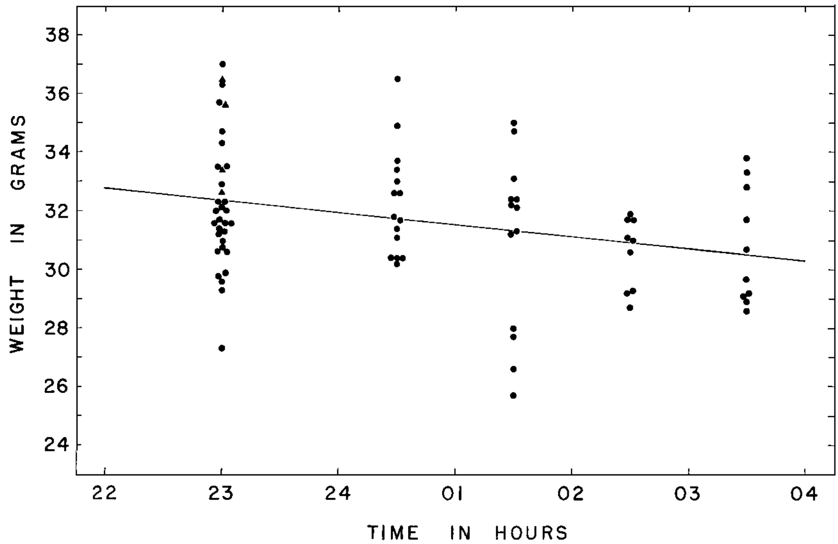

Figure 1. Weights and estimated arrival times of Veeries during the night of 6–7 May 1965. Circles indicate weights of birds trapped; triangles weights of birds killed. Weights of trapped birds include corrections (see text). The regression line for weight on time is shown; it has a slope of –0.41 g/hr.

and Massey (1957) and other textbooks. The conventional 5 per cent probability level is used to indicate significance.

Results

Weights of 80 Veeries and their estimated times of arrival or kill on the night of 6–7 May 1965 are shown in Figure 1. The slope of the linear regression line for weight on time represents a rate of weight loss of 0.41 g/hr (standard deviation 0.150) and is significantly different from zero. If the mean weight of the Veeries is taken as 31.5 g, which is the mean weight predicted from the regression line at the midpoint of the flight (0100 hours), then the rate of weight loss may be expressed as 1.3 per cent of body wt/hr.

A similar set of results for Ovenbirds on the night of 21–22 September 1966 is shown in Figure 2. The total sample of 96 contained 69 adults, 25 immatures, and 2 that could not be aged. Regressions were calculated for adults and immatures separately, and for the entire sample. The slope of the regression was significantly different from zero for the adults but not for the immatures. A test to determine whether or not any difference exists between the regression lines for adults and immatures (Dixon and Massey, 1957: 218) showed that the two sets of data do not differ sig-

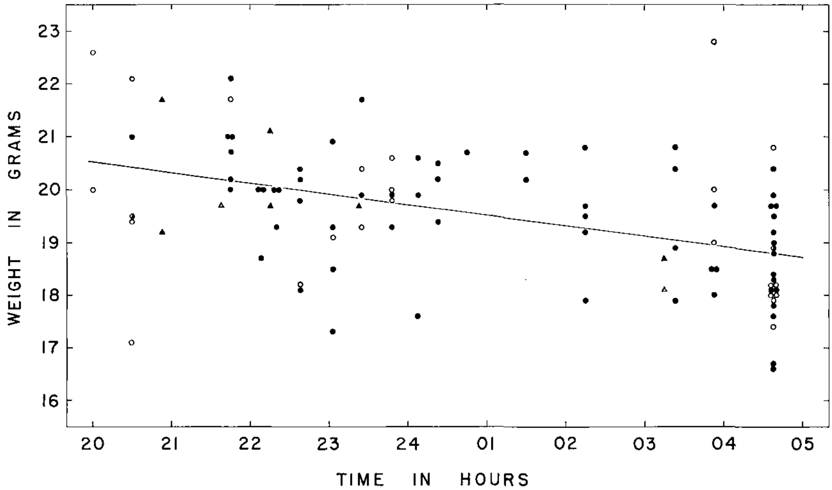

Figure 2. Weights and estimated arrival times of Ovenbirds during the night of 21–22 September 1966. Circles indicate weights of birds trapped; triangles weights of birds killed. Solid symbols are used for adults and open symbols for immatures. Half-solid circles represent weights of trapped birds which could not be aged. Weights of trapped birds include corrections (see text). The regression line for weight on time for the entire sample is shown; it has a slope of –0.20 g/hr.

nificantly. Consequently, I am justified in combining adults and immatures in a single sample. The regression line for the combined sample (including the two birds that could not be aged) is shown in Figure 2, and its slope is significantly different from zero. The rate of weight loss for the adults alone was 0.22 g/hr (standard deviation 0.046) and for the combined sample it was 0.20 g/hr (standard deviation 0.040). Using a body weight of 19.6 g, which is predicted by the regressions for both samples at the midpoint of the flight (0030 hours), the rate of weight loss was 1.1 per cent of body wt/hr for the adults and 1.0 per cent of body wt/hr for the combined sample.

The results are summarized in Table 1, which includes 95 per cent confidence limits for rate of weight loss for the three samples whose mean rates were significantly different from zero. The confidence limits are rather wide, probably as a result of the small size of the samples and the high variability within the populations.

To investigate the possibility that changes in weight with time might have been due to differences in the mean body size of birds arriving at different times, it was assumed that wing chord could be used as a measure of body size, and regressions of wing chord on time were calculated corresponding to each of the four regressions for weight on time. In no case

TABLE 1

ESTIMATES OF WEIGHT LOSS

Sample	Sample size	Rate of weight loss (g/hr) Mean	95 per cent confidence limits	P^1	Mean body weight (g)[2]	Mean rate of weight loss (per cent body wt/hr)
Veery	80	0.41	0.11–0.71	< 0.01	31.5	1.3
Ovenbird:						
Adults	69	0.22	0.13–0.31	< 0.001	19.6	1.1
Immatures	25	0.18		> 0.05	19.6	
All	96	0.20	0.12–0.28	< 0.001	19.6	1.0

[1] Probability that mean rate of weight loss (g/hr) equals zero.

[2] Mean body weight predicted from the regression at the midpoint of the flight: 0100 hours for the Veeries and 0030 hours for the Ovenbirds.

was there a significant trend of wing chord with time, so I conclude that the weight changes during the night did not result from differences in the mean body size of birds arriving at different times.

Discussion

The reliability of the results for weight loss depends primarily on the accuracy of the underlying assumptions, and while these assumptions do not appear unreasonable, little evidence is available to support them.

A modification might be made in the first assumption if it were assumed that groups of birds arriving at the lighthouse at different times started their flights at the same mean time relative to sunset. A correction could then be made to allow for differences in sunset time at the starting points of birds arriving at different times. This would involve additional highly speculative assumptions about the speed and direction of flight, and as the resulting corrections would be small it seems better to omit them, especially as the weight loss determinations are themselves rather imprecise.

Nisbet (1963) summarizes field estimates of rates of weight loss in migrating birds. Omitting one dubious estimate of 3.3 per cent of body wt/hr, eight estimates for various small passerines vary from 0.56 to 1.8 per cent of body wt/hr, but six of these are less than 1.0 per cent of body wt/hr. Most of these estimates were based on small samples with some highly questionable assumptions, so the wide range of variation is not surprising. That the estimates for Veeries and Ovenbirds from the Long Point Lighthouse fall in a relatively narrow range (1.0 to 1.3 per cent of body wt/hr) is satisfactory, but it is not clear why most of Nisbet's estimates are lower than this.

Nisbet's (1963) estimate of 1.8 per cent loss of body wt/hr was based on his recalculation of the data of Graber and Graber (1962) for Swainson's and Gray-cheeked Thrushes (*Hylocichla ustulata* and *H. minima*) killed at a television tower in Illinois. The calculations were based on small samples killed at different times on different dates in different years, so an accurate result cannot be expected. If the largest of the Grabers' samples (32 adult male Swainson's Thrushes) is considered alone, the recalculated rate of weight loss is 1.6 per cent of body wt/hr. This is reasonably close to the 1.3 per cent loss of body wt/hr obtained for the Veery at Long Point.

Another field estimate by Raveling and LeFebvre (1967) from weights of 38 Tennessee Warblers (*Vermivora peregrina*) killed at a Wisconsin television tower on the night of 2–3 October 1962 shows a mean rate of weight loss of 0.2 g/hr or 1.83 per cent of mean body wt/hr. As the sample was small and the calculation involved assumptions about the time of kill, this is probably not a precise determination. It may be noted that the results reported here for the Veery and the Ovenbird are based on the largest samples for which appropriate data have been obtained at the Long Point Lighthouse. Several smaller samples were rejected because they did not show significant relationships between weight and time.

LeFebvre (1964) determined energy expenditure of homing pigeons (*Columba livia*) using doubly-labeled water (D_2O^{18}). The mean rate of weight loss for eight birds was 3.53 g/hr or 0.9 per cent of body wt/hr during an average flight time of 8.6 hours (LeFebvre, pers. comm.). Pearson (1964) determined weight loss in Tippler pigeons. Six birds that flew for 4.13 hours lost an average of 1.76 per cent of initial body wt/hr and four that flew for 3.17 hours lost 1.36 per cent of initial body wt/hr. Nine birds that had the cloaca experimentally sealed flew for an average of 4.33 hours and lost 1.19 per cent of initial body wt/hr.

There is no evidence to indicate the composition of the weight loss in the Long Point birds. Loss of fecal material would probably be negligible in nocturnal migrants that presumably had been flying for a considerable time before measurements were started. Urinary output is also not likely to be significant. If it is assumed that the birds are metabolizing fat, then the weight of carbon dioxide produced will approximately balance the weight of oxygen consumed, so most of the weight loss must be in the form of water. The weight of metabolic water produced will approximate the weight of fat metabolized, but it will not necessarily equal the weight of water lost. It is probable that the rate of water loss will be influenced by other factors, such as the ventilation rate, that are not primarily dependent on the rate of production of metabolic water. Odum et al. (1964) believe that total body water and other nonlipid components of migrating birds are essentially homeostatic. If this view is accepted, then energy expenditure during flight can be calculated from the weight loss following the procedure used by Nisbet et al. (1963) and Raveling and LeFebvre (1967). If the weight loss was equal to depletion of fat (calorific value 9.5 kcal/g), the mean rate of energy expenditure for the Veeries was 0.12 kcal/(g·hr), for the adult Ovenbirds 0.11 kcal/(g·hr) and for the combined sample of adult and immature Ovenbirds 0.10 kcal/(g·hr). It should be emphasized that these estimates are tentative, as they are based on the assumption that the weight loss is equivalent to the weight of fat metabolized, which, as pointed out above, may not be strictly true.

The ratio of flight metabolism to standard metabolism may be estimated if the equation provided by Lasiewski and Dawson (1967: 18, equation e) is used to calculate the standard metabolism of the Veeries and Ovenbirds. The ratio is 8.8 for the Veery, 6.7 for the adult Ovenbirds, and 6.1 for the combined sample of adult and immature Ovenbirds.

Three direct measurements of flight metabolism are available for comparison. The flight metabolism of pigeons, determined by means of isotopically labeled water, was 0.058 kcal/(g·hr) for birds of 384 g mean weight (LeFebvre, 1964). This was about 8 times the estimated resting metabolic rate of these birds, but was about 13 times the mean standard metabolic rate for the domestic pigeon calculated from the four values quoted by Lasiewski and Dawson (1967). Tucker (1966) measured the oxygen consumption of Budgerigars (*Melopsittacus undulatus*) flying in a wind tunnel. Assuming a caloric equivalent of 4.8 kcal/liter of oxygen, the mean energy expenditures of birds flying at 32 km/hr were 0.186 kcal/(g·hr) and 0.205 kcal/(g·hr) for Budgerigars weighing 42 g and 32 g, respectively. Tucker did not give results for standard metabolism, but he indicated that oxygen consumption in flight was about 6 times that of birds sitting quietly in the wind tunnel. If the standard metabolism is calculated from the equation for nonpasserines provided by Lasiewski and Dawson (1967: 18, equation f), the flight metabolism of Tucker's Budgerigars was about 24 times the standard metabolic rate. Lasiewski (1963) measured the oxygen consumption of a Costa's Hummingbird (*Calypte costae*) weighing 3.0 g, during 35 minutes of hovering flight at an ambient temperature of 24°C. Its flight metabolism, calculated from Lasiewski's data, was 0.204 kcal/(g·hr). This was about 7 times greater than its resting metabolism at the same ambient temperature, but about 14 times the standard metabolic rate in thermoneutral surroundings. On a weight-specific basis the estimates of flight metabolism for the Veery and Ovenbird are intermediate between the direct determination for the pigeon and those for the hummingbird and Budgerigar. These determinations of flight energy cover a wide range of values, and manifestly further work is necessary before their significance can be properly evaluated.

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SUMMARY

Mean rates of weight loss during migratory flight were estimated for nocturnal migrants trapped or killed at the Long Point Lighthouse, Ontario. Estimates were based on the assumption that differences between the mean weights of birds arriving at the lighthouse at different times on the same night were the same as the mean weight changes of individual birds flying during the same time intervals. A sample of 80 Veeries on the night of 6–7 May 1965 had a mean rate of weight loss of 0.41 g/hr; a sample of 96 Ovenbirds on 21–22 September 1966 gave a mean rate of weight loss of 0.20 g/hr. Expressed as a percentage of mean body weight, the rate of weight loss was 1.3 per cent/hr for the Veery and 1.0 per cent/hr for the Ovenbird. Most other field estimates of weight loss in migrating birds are in the range 0.56 to 1.8 per cent of body wt/hr.

If it is assumed that weight loss is equivalent to fat depletion, then flight metabolism can be estimated as 0.12 kcal/(g·hr) for the Veery and 0.10 kcal/(g·hr) for the Ovenbird. These results are compared with estimated standard metabolic rates in the same species, and with direct determinations of flight metabolism in other species.

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