

WEIGHT-LOSS DURING MIGRATION

PART II: REVIEW OF OTHER ESTIMATES

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In Part I an estimate was obtained of the rate of weight-loss of Blackpoll Warblers during a long non-stop flight. In Part II this estimate will be compared with eight field measurements of weight-loss in other species, and with nine theoretical calculations (four of which are previously unpublished) of the power consumption of flying birds.

FIELD MEASUREMENTS OF WEIGHT-LOSS

Blackpoll Warblers crossing the western North Atlantic

In Part I the rate of weight-loss of Blackpoll Warblers was estimated to be about 0.56 ± 0.07 percent of mean weight per hour. The chief limitations of this estimate are (a) the lack of direct measurements of the departure weight, and (b) the small samples of both departing and arriving birds, reflected in the large standard error. In future years attempts will be made to overcome these limitations, but it will be difficult to do so without sacrificing the precise measurement of flight-time, one of the main advantages of this study over the others quoted here.

Robins crossing the North Sea

Butterfield (1952) summarized weights of birds caught at Lista, South Norway, and Fair Isle, Shetland, Great Britain, between 28 September and 3 October 1951. The average weight of 20 Robins (*Erithacus rubecula*) caught at Lista was 17.72 ± 0.22 gm., and that of 24 Robins caught at Fair Isle was 14.92 ± 0.29 gm.; the difference was 2.80 gm., or 17.2 ± 2.2 percent of the mean weight. According to Hyatt and Mylne (1952) nearly all the Lista Robins were caught at the lighthouse on the night of 28-29 September, and according to P. Davis (*in litt.*) nearly all the Fair Isle Robins were caught on 1 and 2 October. The Fair Isle birds were weighed immediately after capture (K. Williamson *in litt.*), but some of the Lista birds were not weighed for several hours (C. K. Mylne, pers. comm.), and must have lost some weight during this period.

Migration in these few days of 1951 has been discussed by several authors. Jenkins (1953) showed that Robins (and other species) arrived in southern Scandinavia on the mornings of 28 and 29 September, and were then held up by fog until the evening of 30 September, when many departed and were drifted westwards into the British Isles. Williamson (1952) suggested that the birds oriented down-wind after meeting fog in the Skagerak and Kattegat, and Yapp (1956), although criticizing Williamson's theory, also assumed that the birds flew down-wind. Lack (1960), however, gave evidence that drift-migrants which reach England from Scandinavia do not

normally fly down-wind, and Bourne (pers. comm.), using radar, has observed that those which reach Scotland usually head S.S.W. while crossing the North Sea. On the basis of Bourne's observations, and the weather map published by Jenkins (1953), it seems probable that the Robins which reached Fair Isle on 1 October 1951 had taken off somewhere in the southern half of Norway on the preceding evening. Nisbet (1957) has shown that, in weather conditions similar to those which prevailed on 28 and 29 September 1951, birds trapped at Lista have provided a good sample of those which migrate into southern Norway from the N. N. E. However, the birds which reached Fair Isle may also have included some which had bred in south-central Scandinavia and which had not migrated before 30 September, and these would probably have been heavier than those caught at Lista. Hence the difference in weights between the birds caught at Lista and at Fair Isle may under-estimate the loss in weight during the crossing of the North Sea.

According to the log of the Fair Isle Bird Observatory (P. Davis *in litt.*), one Robin was trapped at 0600 (G. M. T.) on 1 October, but most of the birds were trapped between 1200 and 1900 on that day and in the early morning of the 2nd. Davis reports that most birds which arrive at Fair Isle pass quickly through the trapping area to other parts of the island, so that most are caught within a few hours of arrival. Hence the average arrival time of the birds trapped was probably about 1330 (± 2 hours). Assuming that they took off about 18.00 (about 45 minutes after local sunset) on the preceding evening, we estimate their time of flight to have been about 19.5 ± 2 hours. Thus their average rate of loss of weight was probably about $0.88 \pm .15$ percent of mean weight per hour.

Butterfield (1952) also quoted weights of five other species, but in four cases the samples were small and the arrivals at Fair Isle were spread over several days. In the fifth case, the Goldcrest (*Regulus regulus*), the Lista birds were heavier by 8.0 ± 3.9 per cent of mean weight, and the Fair Isle birds were all trapped in the early morning of 1 October, probably after 11-12 hours' flight. Hence their average rate of loss of weight was probably about $0.7 \pm .4$ percent of mean weight per hour.

In a separate study, Davis (1962) summarized the weights of 69 Robins which were caught at Fair Isle on days of large arrivals in various years, and recaptured on subsequent days. The groups which stayed longest (6-20 days) gained, on average, 18 percent of their initial weight in spring, and 17 percent of their initial weight in autumn. If it is assumed that these gains in weight were approximately the same as the birds' losses during their flight to Fair Isle, the average loss would be 16 ± 2 percent (standard error estimated) of their mean weight during flight. This is likely to be an under-estimate, since some of the birds may have left Fair Isle without replacing all their fat. Records supplied by Davis (*in litt.*) indicate that on the days when these birds were first trapped, Robins were sometimes trapped mainly in the early morning, and sometimes mainly in the late evening, while on many days there was evidence that arrivals continued for several hours during the day; my esti-

mate of the average time of arrival is about 1250 G. M. T. (± 0.6 hours). Assuming that the birds took off between a half and one hour after sunset on the previous day, the average time of flight would then be about 18.6 ± 0.7 hours. Hence a low estimate of the rate of weight loss is $0.86 \pm .11$ percent of mean weight per hour.

Greenland Wheatears crossing the Atlantic

Williamson (1958, 1961) showed that Greenland Wheatears (*Oenanthe oe. leucorhoa*) arrive in the British Isles in autumn during westerly winds associated with Lows near Iceland, their average weights (measured at Fair Isle) being relatively high (25-27 gm.) when the birds have strong tail-winds (from the northwest), and relatively low (21-23 gm.) when the winds are light or from the north or southwest during part of the crossing. Assuming that the birds cross from south-east Greenland, that they fly at 26 knots air-speed and that they are affected by the surface winds, Williamson calculated that their flight-times vary between 24 and 40 hours. Lack (1959) disputed Williamson's interpretation of the birds' behavior, but the dispute scarcely affects the estimates of flight-times (Williamson 1961).

Wheatears have not been weighed before leaving Greenland, but Williamson pointed out that they often attain weights of "close on 40 gm." before crossing the Atlantic in spring. The heaviest group of spring migrants trapped on Fair Isle averaged 37.75 gm. (Williamson 1959). Assuming the mean departure weight in autumn to be similar (say 38 gm.), the mean arrival weight to be 24 gm., and the mean flight-time to be 34 hours, the average rate of weight-loss is about 1.3 percent of mean weight per hour. This is more likely to be an over-estimate than an under-estimate, because the main range of the Greenland Wheatear is west and north of the assumed departure area.

P. Davis (*in litt.*) has supplied weights of Greenland Wheatears caught on Fair Isle on 21 September 1959, when more than 1,000 birds arrived on the island—a larger 'fall' than any discussed by Williamson. The average weight of 62 birds trapped was 30.77 ± 0.38 gm., representing a loss of about 7.2 gm., if we assume the departure weight to have been 38 gm. Most of the birds were trapped in the early morning (from dawn onwards) and only four had been trapped on the preceding afternoon. If we assume that most of the birds arrived during the six hours before dawn on 21 September, and that they had taken off about one hour after sunset in southern Greenland on 19 September, their flight time would be about 28 hours: this is consistent with Williamson's assumptions and the published weather maps for the period. Hence their average rate of weight-loss is estimated to be about 0.75 percent of mean weight per hour.

Both these estimates are very rough, because of the lack of direct evidence about departure-weights and flight-times, but so many arrival weights are now available that this is a very promising species for future study.

Weights before and after a night of migration

Helms (1959) weighed Song Sparrows (*Melospiza melodia*) at Plum Island, Massachusetts, before and after the night of 5/6 April 1958, when there was a large migration of the species. The average weight of 40 birds caught on the morning of 6 April was 21.13 ± 0.20 gm. Twenty-four birds caught on the afternoon of 5 April averaged 22.85 ± 0.41 gm.; including 48 birds caught in the morning the average weight for 5 April was 22.62 ± 0.20 gm. (Four birds caught on both days have been excluded from these averages, but were included in Helms' original figures.) Helms gave evidence that most or all of the population sampled on 5 April left and was replaced by a new population, since of the four birds caught on both days "two were residents and two had been weakened by our taking of blood samples". Another piece of evidence against extensive mixing of two populations is that the variance of the weights was the same on the two days. Then, if it is assumed that the new population weighed the same on 5 April as the old population, its loss in weight during the night was 1.72 ± 0.46 gm., or 1.49 ± 0.28 gm., according to the figure chosen for the mean weight on the 5th. Subsequent work with radar has shown that on warm cloudy nights in early April (such as that of 5/6 April 1958), birds usually migrate for between 10 and 11 hours (Drury and Keith 1962). Hence we estimate the loss in weight of the Song Sparrows to be about 0.69 ± 0.14 percent of mean weight per hour. This is probably an underestimate, since some birds may have stayed at Plum Island overnight.

Birds on ocean weather ships

Eliassen and Hjelmtvedt (1958) weighed 26 birds of 14 species caught on weather ships in the North Atlantic ocean. They estimated their weight-loss by comparing their observed weights with the maxima given by Groebbels *et al.* (1938), and estimated (for 21 birds) the time of flight by means of various assumptions about their flight-speeds and the way in which they were drifted away from their migration routes. The resulting estimates of the rate of weight-loss vary between 1.4 percent and 6.2 percent of mean weight per hour, the average being 3.3 ± 0.37 percent. These high figures cannot be accepted, however, because:

1. The maximum weights given by Groebbels *et al.* may exceed the average departure weights of the species concerned;
2. The birds which stop on small ships are probably lighter than the bulk of the population;
3. The set of assumptions made about the birds' migration is only one of a number of alternatives, and leads to impossible conclusions (e. g. that *Fringilla coelebs*, *Alauda arvensis* and *Sturnus vulgaris* migrate W. N. W. from Norway in spring).

Thrushes killed at two different times in the night

Graber and Graber (1962) compared the weights of thrushes (*Hylocichla* spp.) killed at a television tower in Illinois at about 0500 on 19 September 1960, and between 0030 and 0200 on 29 September 1959. In a sample of 32 adult male *H. ustulata*, the 1959 group was heavier, on average, than the 1960 group by 1.7 ± 0.66 gm., or 5.5 ± 2.1 percent of the mean weight (31.4 gm.). In samples of 24 adult female *H. ustulata* and 13 adult male *H. minima*, the corresponding differences were 7.3 percent and 6.9 percent respectively. The average difference for the three samples was thus about 6.4 ± 1.8 percent (standard error estimated). Assuming that the weights of the two populations were the same when they started their migrations, and that the 1960 sample had flown for 3.5 \pm 0.6 hours longer (sunset was 17 minutes earlier on 28 than on 18 September), the average rate of weight-loss is 1.8 ± 0.6 percent per hour. (Graber and Graber themselves rejected this estimate, and quoted higher figures based on the weights of extreme individuals, but this is statistically illegitimate.) This is a very rough estimate, but the method is promising.

Summary of field-measurements

The above estimates of rates of weight-loss are summarized in Table 9. With the exception of Eliassen and Hjelmvedt's dubious estimate, and the Grabers' rough one, all the field-estimates of the rate of weight-loss are grouped between 0.56 percent and 1.3 percent of total weight per hour. All these estimates depend on more or less dubious assumptions, and all have a fairly large standard error (because they all depend on the measurement of small differences in variable populations). However, the close grouping of the results obtained by widely different methods is encouraging, and it seems reasonable to conclude that the average rate of weight-loss in

TABLE 9. FIELD-ESTIMATES OF THE RATE OF WEIGHT-LOSS
IN MIGRATING BIRDS.

Author	Species	Weight-loss (% of total weight per hour)
This paper (Part I)	<i>Dendroica striata</i>	0.56 \pm .07
Butterfield 1952	<i>Erithacus rubecula</i>	0.88 \pm .15
Butterfield 1952	<i>Regulus regulus</i>	0.7 \pm .4
Davis 1962	<i>Erithacus rubecula</i>	0.86 \pm .11
Williamson 1958, 1961	<i>Oenanthe oenanthe</i>	ca. 1.3
This paper (Davis <i>in litt.</i>)	<i>Oenanthe oenanthe</i>	ca. 0.75
Helms 1959	<i>Melospiza melodia</i>	0.69 \pm .14
Eliassen and Hjelmvedt 1958	various	3.3 \pm 0.37
Graber and Graber 1962	<i>Hylocichla</i> spp.	1.8 \pm 0.6

Note. These figures are calculated from the data published in the papers quoted. Except for Graber and Graber (1962), none of the authors actually estimated the rate of weight-loss. All the estimates depend on assumptions which are discussed in the text.

migrating passerines is of the order of 0.8 percent of total body-weight per hour. There is also evidence for interspecific differences in rate of weight-loss: for example, the maximum estimate for the Blackpoll Warbler is appreciably less than the minimum estimate for the Robin.

In Part I it was argued that the observed weight-loss of the Blackpoll Warblers represented consumption of fat, and that consumption of carbohydrate and loss of water were negligible. Strictly, these arguments apply only to long-distance migrants, but if we assume that they are valid for all the species discussed above, the figure of 0.8 percent of total weight per hour for their average rate of weight-loss corresponds to an average power consumption of about 0.076 Kcal./gm. total weight/hr. Assuming (as in Part I) the average resting power consumption to be 0.045 Kcal./gm. fat-free weight/hr., this figure is about 1.7 times the resting power consumption when the bird is lean, and about 3.4 times the resting power consumption when half the bird's weight is fat. If some of the birds lost water during flight, these figures will be slightly too high.

A LABORATORY MEASUREMENT OF POWER CONSUMPTION

Lasiewski (1962) measured the oxygen consumption of a Costa's Hummingbird (*Calypte costae*) hovering continuously for 50 minutes in a bell-jar at 24° C. Determinations during one-minute intervals varied from 32.7 to 50.9 cc. oxygen/gm. total weight/hr., the average over 35 minutes being 42.4; the standard error was not stated, but the figures given suggest that it was about 0.7. Unfortunately it is not known whether the bird was using carbohydrate (5.05 Kcal./liter O₂) or fat (4.69 Kcal./liter O₂); it may be guessed that it consumed largely carbohydrate at the start of the flight, and largely fat at the end. Assuming a mean value of 4.85 ± 0.08 Kcal./liter O₂, the mean power consumption is $0.206 \pm .005$ Kcal./gm. total weight/hr., or about 3.3 ± 0.3 times the mean of the figures obtained by Pearson (1950) for the rates of metabolism of resting hummingbirds of two other species. This is about 2.7 times the power consumption suggested above for migrating passerines, which accords with the intuitive idea that hovering is a more strenuous activity than forward flight.

THEORETICAL CALCULATIONS OF POWER CONSUMPTION

In accordance with the terminology adopted in Part I, the term "power output" is used for the rate at which the flying bird does work on the air, and the term "power consumption" for the total rate at which it releases energy (including heat in the muscles, etc.). Some theories of bird flight give estimates of power output, some of power consumption, and some of the ratio of power consumption in flight to that at rest. In order to permit comparisons the following assumptions are made in this paper:

1. The efficiency of birds' flight muscles is 22 percent, and all the wasted power can be used to warm the body.

2. The power consumption of small birds at rest at 10° C. is about 0.045 Kcal./gm. fat-free weight/hour, irrespective of the amount of fat they carry. For resting hummingbirds I have used Pearson's (1950) figure of 0.062 Kcal./gm./hour, and for resting pigeons I have used the figure of 0.0079 Kcal./gm./hour quoted by Zeuthen (1942).

Where possible, I have quoted estimates of the power consumption (a) of a hovering hummingbird, (b) of a 10-gm. bird without fat, (c) of the same bird carrying 10 gm. of fat. Some of the theories predict the dependence of power consumption on the total weight of the birds: for those that do not, I have assumed that the power output is proportional to the total weight.* Hence the power consumption predicted for case (c) is usually twice that predicted for case (b), subject to the consideration, mentioned in Part I, that enough power must always be expended to maintain the body temperature.

The theory of Zeuthen

Zeuthen (1942) published some estimates of the power output of a flying pigeon (body-weight 290 gm.) at various air-speeds. The estimates increased from 0.0041 Kcal./gm. total weight/hour at a speed of 30 km./hr. to 0.051† Kcal./gm. total weight/hour at 70 km./hr. Unfortunately, Zeuthen did not state how these figures were obtained (except that the calculation was "carried out in co-operation with the aircraft engineer K. G. Zeuthen"), but since his figures for power output are proportional to the cube of the air-speed it was evidently assumed that the drag is proportional to the square of the air-speed. Although this assumption would be valid for a floating body (e.g. an airship or a fish), the drag on a lifting wing depends chiefly on the lift-drag ratio and varies only slowly with the air-speed. Hence Zeuthen's figures are probably too high, at least for the higher air-speeds. Indeed, Zeuthen himself showed that if a pigeon were to consume power at the rate he predicted, it could not dissipate all the heat produced in the muscles by conduction and radiation alone, but must also evaporate water in order to regulate its body temperature. Salt and Zeuthen (1960) estimated the rate at which water must be evaporated at 70 km./hour air-speed (a normal flight-speed for pigeons, according to Meinertzhagen 1955) to be about 22 percent of total body-weight per hour. Such a rate of water-loss is obviously quite impossible for a migratory species.

*Note that this assumption is made only for birds of the same species: it may not apply to birds of different species because their wing-areas, styles of flight, etc., may differ as well as their weights. The dependence of power output on size among different species will be discussed at the end of this paper.

†This estimate is misprinted in Zeuthen's original table (total power output printed as 17.8 instead of 14.8 Kcal./hr.). Most of Zeuthen's figures (including the misprint) have been republished by Salt & Zeuthen (1960).

A new theory based on water-retention

Salt and Zeuthen's calculation can be adapted to yield an estimate of the maximum possible rate of power consumption, above which water-loss would prevent long-distance migration. Kendeigh's (1944) experiments on the resting House Sparrow suggest that at 10° C. about 10 percent of the power consumption is eliminated by evaporation*, and hence about 90 percent by conduction and radiation. Assuming that the same is true for a migratory bird of 10 gm. fat-free weight, the power eliminated by conduction and radiation is about 0.405 Kcal./hour. Zeuthen (1942) and Salt and Zeuthen (1960) suggested that in flight a pigeon might increase its conduction and radiation losses by a factor of not more than 5; let us assume that this maximum factor is also 5 for a 10-gm. bird when lean, but is only 4 when it is fat because of greater insulation. Assume further that the maximum permissible rate of water-loss for a long-distance migrant is 0.02 gm./hour (15 percent of fat-free weight in a 75-hour flight), so that the maximum power loss by evaporation is 0.011 Kcal./hour. Thus the maximum permissible power loss in flight is 2.036 Kcal./hour when lean and 1.631 Kcal./hour when fat. Assuming 22 percent muscular efficiency, the maximum permissible power consumption is then about 2.61 Kcal./hour (5.8 times the resting power consumption) for a lean bird, and 2.09 Kcal./hour (4.6 times the resting power consumption) for a fat bird. If the fat bird has 10 gm. of fat this is about 0.104 Kcal./gm. total weight/hour, which is close to some of the higher field-estimates of weight-loss, e.g. Williamson's figures for the Greenland Wheatear.

The theory of Odum

Odum (1960) based his theory on the experiments of Pearson (1950, 1954), which suggested that a hummingbird (*Calypte anna*) used about 2.4 times as much power while hovering as during daytime activity in the field, and about 6 times as much power while hovering as while resting. Odum pointed out that these figures are similar to the ratios observed in horses and men for the ratios between power consumption during sustained hard work, moderate work and resting respectively. He therefore suggested that similar figures should apply to other small birds, so that a bird in steady flight should use energy at between two and four times the "existence" rate. The latter is defined as the average rate at which the bird uses energy to maintain itself (including food-seeking), and Odum adopted a figure of 0.05 Kcal./fat-free gm./hour—about 10 percent more than the figure used in this paper for the power consumption of a *resting* bird at 10° C. Hence Odum estimated that migrating birds should consume between 0.1 and 0.2 Kcal./fat-free gm. / hour.

*The water which this represents is approximately replaced by metabolic water from combustion of fat. However, the latent heat of evaporation is "eliminated" in the sense that, if the water were retained or eliminated as liquid, more heat would have to be lost by radiation and conduction in order to regulate the bird's temperature.

Although Odum stated that the numerical estimates in his 1960 paper had been adjusted to allow for the increase in power consumption with increase in body-weight, his figures for the power consumption of a fat bird were exactly the same as those for a lean bird. In a later paper, Odum, Connell and Stoddard (1961) incorporated a correction by publishing two curves, one based on the assumption that the ratio of flight power consumption to resting consumption is 2.0 when the bird is lean and increases proportional to the total weight of the bird, the other based on the assumption that the ratio is 3.0 whether the bird is fat or lean. The second curve in fact represents an expenditure of 0.15 Kcal./gm. total weight/hour when the bird is lean, falling to 0.075 Kcal./gm. total weight/hour when it is fat; the first represents an expenditure of 0.10 Kcal./gm. total weight/hour irrespective of weight. These estimates are thus lower than those of Odum (1960) for lean birds, but higher for fat birds. Some reduction has subsequently been justified by the work of Lasiewski (1962), who showed that the ratio of hovering power consumption to resting consumption for hummingbirds is much less than Pearson's estimate of six, and is probably about 3.3. Thus the best current estimates from Odum's theory are those for fat birds, 0.075-0.10 Kcal./gm. total weight/hour.

Odum's theory has been criticized by Yapp (1962), on the grounds:

1. that Pearson's measurements were too inaccurate and variable for reliable conclusions;
2. that Pearson's hummingbirds were probably in oxygen debt;
3. that the analogy between horses, hummingbirds and humans is unsound.

The first two of these objections have now been answered, since Lasiewski's measurement of the power consumption of a hummingbird was reliable and based on 50 minutes' continuous hovering. The third objection is answered by the fact that Odum's figures now depend, not on the analogy between birds and mammals, but upon the comparison between hummingbirds and other small birds.

Yapp's theory of flapping flight

Yapp (1956) estimated the power required for flapping flight by means of mechanical arguments. His model of flapping flight assumed: (1) that the bird falls freely during the upstroke of the wings; (2) that air resistance is negligible. Hence the theory is more appropriate to hovering than to forward flight, because in forward flight the bird probably gains much more energy from lift during the upstroke than it loses to drag during both strokes.

Yapp further assumed: (3) that the bird falls freely for a time $1/2n$, where n is the number of wing-beats per second; (4) that its energy requirement per wing-beat is equal to the potential energy lost in this fall; (5) that the muscular efficiency is 20 percent (intended to be a low estimate). In making assumption (4), Yapp overlooked the energy required to arrest the bird's fall at the beginning of the downstroke. If the bird's fall is stopped with a jerk after

$1/2n$ seconds, this overlooked energy would be equal to that calculated by Yapp; if the wing-beat is smooth (the bird starting the downstroke after falling for $1/4n$ seconds), however, Yapp's estimate would be about right. The wing-beat of small birds is probably slightly jerky, since stroboscopic measurements quoted by Greenewalt (1960a) indicated that the downstroke of a chickadee (*Parus carolinensis*) lasts 50 percent longer than the upstroke. Hence I suggest that the power required by Yapp's model is about 30 percent larger than Yapp's estimate. Making this amendment, the power required by the bird is, on Yapp's theory, $0.067 M/nF$ Kcal./hour, where M is the bird's weight in grams, and F is a quantity referred to by Yapp as "aerodynamic efficiency" and assumed by him to be about 0.5. For small passerines n is about 20 (Greenewalt 1960b: Yapp used a figure of 5 from Meinertzhagen 1955), so that for a 10-gm. bird this is about 0.067 Kcal./hour when it is lean and 0.134 Kcal./hour when it carries 10 gm. of fat. 80 percent of this power is assumed to be wasted in the muscles, and therefore goes towards the power required for warming the body. Using my figure of 0.045 Kcal./fat-free gm./hour for the latter (Yapp used 0.04), I estimate the total power consumption of the 10-gm. bird in flight as 0.463 Kcal./hour when lean and 0.477 when fat, respectively 1.030 and 1.060 times the resting power consumption. For hummingbirds n is typically about 35 (Greenewalt 1960c), and Yapp's theory then predicts a ratio of only about 1.012, contrasting with Lasiewski's experimental estimate of 3.3.

Modification of Yapp's theory

The discrepancy is probably due to Yapp's interpretation of F as efficiency. F is the ratio between the energy gained by the bird during the downstroke and the work it does on the air, and can be written as follows:

$$F = \frac{E_b}{E_b + E_a/e},$$

where e is the true aerodynamic efficiency, measuring the proportion of the energy transferred to the air which helps to support the bird, and E_a is the energy which must be imparted to the air for the bird to gain energy E_b . In a simplified model, a mass m of air is accelerated to a downward velocity u in order to change the bird's velocity from U downwards to U upwards. Then, by momentum considerations,

$$m u = 2 M U,$$

$$\text{and, since } \frac{E_a}{E_b} = \frac{m u^2}{2 M U^2},$$

$$F = (1 + 2M/m e)^{-1}.$$

Now, roughly, $m = \rho At$, where ρ is the density of the air (roughly 1.2×10^{-3} gm./cm.³), A is the wing area and t is the average depth of the wing-stroke. For small birds $2M/m$ is then much greater than one (see below), so it is a reasonable approximation to write:

$$\text{power output} = 0.134 M^2/n e \rho A t \quad \text{Kcal./hour.}$$

For the following two examples values of n and A were obtained from Greenewalt (1960b, c), t was estimated from the diagrams in Greenewalt (1960c), e is assumed to be 0.5, and muscular efficiency is assumed to be 22 percent.

(a) A lean passerine: $M = 10$ gm., $A = 65$ cm.², $n = 20$ strokes/sec., $t = 7.5$ cm. Then power output = 0.22 Kcal./gm./hour, and power consumption = 1.01 Kcal./gm./hour, no less than 22 times the resting value.

(b) A hummingbird: $M = 4$ gm., $A = 19$ cm.², $n = 35$ strokes/sec., $t = 4$ cm. The theory requires slight modification, since both strokes of a hovering hummingbird's wing help to support the body (Greenewalt 1960c), so that the effective value of n is twice the wing-beat frequency, but as the wing is held at an angle such that the volume of air displaced at each half-stroke is only about $\frac{1}{2} A t$ (Greenewalt 1960c), the above formula should still be valid. Then power output = 0.34 Kcal./gm./hour, and power consumption = 1.57 Kcal./gm./hour, about 8 times Lasiewski's experimental value.

Both these estimates are far too high, which suggests that Yapp's assumption that the wing provides no lift during the upstroke is incorrect. It is almost certainly incorrect for forward flight (Brown 1961a): indeed, as von Holst and Kùchemann (1942) pointed out, the body of a flapping bird in fact oscillates very little in the vertical plane, which suggests that some part of the wing provides lift throughout the entire wing-cycle.

Airfoil theories of forward flight

Brown (1961b) summarized attempts to calculate the power output of birds in forward flapping flight by aerodynamic methods. These theories usually assume that the wings provide lift during both strokes, and that the angle of attack of the wings is always reasonably small, so that the drag can be calculated by means of elementary airfoil theory. The most elaborate calculation was that of Walker (1925, 1927), who used a comparatively crude model for the wing-action, but was able to show that his model could fly—in other words that the above assumptions are self-consistent. Then, since the average lift must equal the bird's weight Mg , the average drag is $Mg (C_L/C_D)^{-1}$ where (C_L/C_D) is the lift-drag ratio, averaged over the complete wing-span and the complete wing-cycle. The average power output is $M g v (C_L/C_D)^{-1}$, where v is the average air-speed and the power required to move the wings themselves is neglected. Boel (1929) assumed that (C_L/C_D) is 20, but this is about the maximum estimated by Raspel (1950) for a gliding bird in very favourable circumstances, and is probably much too high for a flapping bird. The difficulty of calculating, or even guessing,

(C_L/C_D) has for long deterred research on these lines (Brown 1961b)

Recently G. W. Schaefer (pers. comm.) has started a new theoretical attack on this problem, using novel observational techniques to study the wing-action. His preliminary results for small birds suggest that (C_L/C_D) is in the neighbourhood of 5, so that if v is 22 knots the power output is estimated to be 0.019 Kcal./gm. total weight/hour. Assuming the muscular efficiency to be 22 percent, the power consumption is estimated to be 0.086 Kcal./gm. total weight/hour, which is in reasonable agreement with the field-estimates quoted in this paper. It is not yet clear how sensitive this estimate is to small details of the assumed wing-action, but the definitive results of Schaefer's calculation may be awaited with interest.

A 'helicopter'-type model of hovering flight

To avoid the above difficulties, I have formulated a theory of hovering flight which takes no specific account of the wing-action. Consider a model in which a hovering bird, of weight M g gm., entrains air, initially at rest, at a rate p gm./sec., and propels it downwards at an average velocity u cm./sec. through an area A cm.², equal to the wing-area. Then

$$p = \rho A u,$$

where ρ is the density of the air. For equilibrium,

$$Mg = pu,$$

so that the power output is

$$p u^2 / 2f = (2f)^{-1} (Mg)^{3/2} (\rho A)^{-1/2},$$

where f is the efficiency of the process, and consists of the product of two quantities, one the proportion of the power output which helps to support the bird, the other reflecting the fact that the air-flow is not uniform. By analogy with the performance of helicopters, we may guess that f is about 0.3. Then, for a 4 gm. hummingbird ($A = 19$ cm.², $\rho = 1.2 \times 10^{-3}$ gm./cm.³), the predicted power output is 0.059 Kcal./gm./hour, and the power consumption 0.27 Kcal./gm./hour, reasonably close to Lasiewski's measured value of 0.206. However, it would be difficult to extend this theory to forward flight without arbitrary assumptions.

Output of flight muscles

Brown (1961a, b) quoted a figure of 0.01 horsepower per pound (0.014 Kcal./hour per gm.) for the maximum output of mammalian muscle, and (1961b) quoted aerodynamic calculations which indicate that the output of birds' flight muscles is several times greater. Weiss-Fogh (1961) stated that birds' flight muscles are six times more powerful than mammals' muscles. Hence for a hummingbird of 4-gm. body-weight, with 1.15 gm. of pectoral muscle (Greenewalt 1960b), the potential power output is 0.096 Kcal./hour, and the potential power consumption is 0.44 Kcal./hour if the muscular efficiency is assumed to be 22 percent. This is only about half

Lasiewski's measured value, which suggests either that Weiss-Fogh's figure of six is too low, or that my figure of 22 percent is too high, or that the weights quoted by Greenewalt omitted a significant part of the muscles which produce the power. Similar calculations by Brown (1961b) were equally inconclusive.

This difficulty can be avoided by assuming Lasiewski's figure, 0.75 Kcal./hour/gm. of pectoral muscle, to be typical of the performance of birds' pectoral muscles. Then, for passerines of 10-gm. lean weight, which typically have about 1.55 gm. of pectoral muscle (Greenewalt 1960b), we estimate the total power consumption to be about 1.16 Kcal./hour. This is 0.116 Kcal./gm. total weight/hour if this consumption is achieved when the bird is lean, but only 0.058 Kcal./gm. total weight/hour if it is not reached until the bird has 10 gm. of fat. The smaller figure is the more probable, since the hovering flight of a hummingbird, and the flight of a very fat passerine, are both strenuous activities. It is reasonable to suppose that the size of a bird's flight muscles is adapted to the maximum power which it needs to expend.

Yapp's theory of increased oxygenation

Yapp (1962) outlined a second theory, based on the assumption that the total power consumption is limited in birds (as it is in man) by the rate of supply of oxygen to the muscles. Then the ratio between the maximum rate of sustained power consumption and the resting rate is x/y , where x is the maximum factor by which the pulse-rate can be increased and y is the maximum factor by which the systolic volume (volume of heart-stroke) can be increased.

Experiments by Eliassen (1963) suggest that when a Great Black-backed Gull (*Larus marinus*) takes flight the pulse rate is unchanged and the pulse pressure increases by a factor of about 2.2. If systolic volume is proportional to the pulse pressure, these experiments would suggest that the rate of supply of oxygen to the muscles is increased for flight by a factor of about 2.2. This is surprisingly low for such a large bird, but it is possible that Eliassen's bird was in oxygen debt during flight. There are no direct observations on smaller birds, but the figures of Odum (1945) suggest that for small passerines x is in the range 1.8 to 2.6 (Yapp suggests 1.6 for hummingbirds); according to Yapp, y is unlikely to exceed about 2.5 (the maximum for man). Hence the ratio between maximum power consumption and resting metabolism is estimated to be about 4 for hummingbirds, and between 4.5 and 6.5 for other small birds. Of course, power consumption in normal flight need not approach the maximum possible for the species.

Summary of theoretical estimates

Estimates of power output and power consumption obtained from the above theories are summarized in Table 10, using the assumptions listed on page 144 to derive comparable figures. The various estimates of power output differ enormously, and those for power consumption vary from far below the lowest field-estimate to far above the highest. Therefore it is reasonable to use the field-estimates,

TABLE 10. THEORETICAL ESTIMATES OF POWER OUTPUT AND POWER CONSUMPTION DURING FLIGHT

Theory	Bird	Power Output Kcal./gm.	Power Consumption total weight/hour	Ratio to resting power consumption
Zeuthen 1942	Pigeon, 30 km./hour	0.0041	0.019	2.4
	Pigeon, 50 km./hour	0.019	0.084	11
	Pigeon, 70 km./hour	0.051	0.23	29
This paper (water retention theory)	Small bird, lean	<0.057	<0.26	<5.8
	Small bird, fat	<0.023	<0.104	<4.6
Odum 1960	Small bird, lean	0.022-0.044	0.1-0.2	2.2-4.4
	Small bird, fat	0.011-0.022	0.05-0.1	2.2-4.4
Odum <i>et al.</i> 1961	Small bird, lean	0.022-0.033	0.1-0.15	2.2-3.3
	Small bird, fat	0.018-0.022	0.075-0.1	3.3-4.4
Yapp 1956	Hummingbird	0.0007	0.0627	1.012
	Small bird, lean	0.0013	0.0463	1.03
	Small bird, fat	0.0013	0.0238	1.06
This paper (modification of Yapp 1956)	Hummingbird	0.34	1.57	26
	Small bird, lean	0.22	1.01	22
	Small bird, fat	0.44	2.02	88
Schaefer in preparation	Small bird, lean	0.019	0.086	1.9
This paper (helicopter model)	Hummingbird	0.059	0.27	4.4

This paper (flight muscles)	Hummingbird	<0.023	<0.105	<1.7
	Small bird, lean	<0.02	<0.116	<2.6
	Small bird, fat	0.013	0.058	2.6
Yapp 1962	Hummingbird	<0.055	<0.25	<4
	Small bird, lean	<0.042-0.064	<0.20-0.29	<4.5-6.5
	Small bird, fat	<0.022-0.32	<0.10-0.15	<4.5-6.5
Observed values:				
Lasiewski 1962	Hummingbird	0.045	0.206	3.3
This paper (suggested mean)	Small birds, mostly fat	0.017	0.076	ca. 2.0

Notes. The primary predictions from each theory are printed in boldface; the other figures are derived from them by means of the assumptions listed on page 144. Most of the figures in this table differ slightly from those given in the original papers; for full details see text.

which are quite closely grouped (Table 9), to check the theories—rather than *vice versa* as was done by Graber and Graber (1962). For this purpose I have listed at the foot of Table 10 Lasiewski's experimental estimate for a hovering hummingbird, and the figure of 0.076 Kcal./gm. total weight/hour proposed earlier as the best average of the field-estimates for migrating passerines. It should be recalled that the latter figure would be an over-estimate if the birds concerned lost water during their flight.

Table 10 shows that Odum *et al.*'s estimates of the power consumption of fat passerines agree well with field observations, but that Odum's theory probably over-estimates the power consumption of lean birds. Similarly, the flight muscle theory gives reasonably good agreement with observation for fat passerines, but it predicts only an upper limit for the power consumption of lean passerines. In any case both these "theories" are based merely on extrapolation from experiments on hummingbirds, and neither throws any light on the aerodynamics or physiology of bird flight.

Of the aerodynamic theories, Yapp's, and my modification of it, both disagree with experiment and should be discarded. The "helicopter" theory is in fair agreement with the one experimental measurement on humming birds, and could perhaps be extended to other hovering species, but it includes an unsupported guess of the efficiency of flight. Schaefer's theory is the most promising for future development, but it will be very difficult to extend it beyond its present rudimentary form.

Zeuthen's calculation is the only one made specifically for a large bird, and raises in an acute form the problem of the dependence of power output on body-weight. Although Zeuthen's estimate of the power consumption *per unit of body-weight* of a pigeon flying at 50 km./hour is very similar to the field-estimates for migrating passerines, Zeuthen himself showed that this power consumption is too high to be permissible physiologically in a bird as large as a pigeon, except for very short periods. Odum's theory assumes that power consumption in flight is proportional to resting power consumption, and Eliassen's (1963) measurements on the Great Black-backed Gull are consistent with this; yet, according to King and Farner (1961), resting power consumption increases no faster than the 0.66 power of the body-weight. Thus physiological arguments suggest that the flight power consumption per unit of body-weight should be much smaller in larger birds—roughly three times smaller in pigeons than in 10 gm. passerines, for example. On the other hand, the aerodynamic theories suggest that flight power consumption per unit of body-weight should be larger in large birds. Nonweiler (quoted by Wilkie 1959), using very general aerodynamic arguments, showed that within groups of dimensionally similar animals (or aircraft), flight power consumption should be proportional to the 1.17 power of total weight. "Similarity" in Nonweiler's sense includes style of flight (e.g. lift-drag ratio) as well as shape, so this result may not apply exactly to birds. Nevertheless the elementary airfoil theory outlined in this paper, which uses the same basic assumptions as Nonweiler's, would only be consistent with the physiological theories if the lift-drag ratio of a pigeon's wing were

five or six times greater than that of a small passerine, and this is extremely improbable. Moreover, in birds of different sizes, the weight of the flight-muscles is exactly proportional to the body-weight (Greenewalt 1960b), which suggests that power consumption is more or less proportional to body-weight. This discrepancy could be investigated experimentally—e.g. by measuring the rate of weight-loss in homing pigeons.

The “physiological” theories estimate the maximum power consumption possible for the organism, rather than the normal consumption during flight, but they nevertheless lead to one interesting conclusion. At least two physiological factors (evaporation of water, supply of oxygen, and probably also size of flight muscles) impose an upper limit to the power consumption of birds, and Table 9 shows that this upper limit (between 0.15 and 0.25 Kcal./fat-free gm./hour) is in fact approached by some very fat migrants. Thus if an inefficient species is to evolve a long-distance migration, it must not only evolve a fat-store and a metabolic system to use it, but it must also evolve an efficient flight to carry the fat without expending too much power in doing so. The Blackpoll Warbler appears to have progressed strikingly far in both directions.

SUMMARY

PART I

1. In September and October 1962, over 2,000 Blackpoll Warblers (*Dendroica striata*) were weighed inland in Massachusetts, and 138 in Bermuda. Some weights obtained in earlier autumns in Massachusetts, Rhode Island and Bermuda are also discussed.

2. Among birds of the same fat-class, adults weighed about 0.4 gm. more than immatures, and were about 1.4 mm. longer in the wing. Males were about 0.5 gm. heavier than females, and about 2.3 mm. longer in the wing, but these figures are approximate as some birds appear to have been assigned to the wrong sex. Among birds of the same fat-class, the average weight increased by 0.10 ± 0.024 gm. for each mm. increase in wing-length. Among birds of the same fat-class and wing-length, adults weighed 0.18 gm. more than immatures. The average fat-free weight of the species is about 11.2 gm., but a number of birds weighing 7.9-10.0 gm. have been caught on islands.

3. During 3-24 September 1962, most birds caught at Round Hill, Massachusetts, weighed only 10-15 gm. Arrivals of light birds followed cold fronts. In late September and early October more heavy birds were caught; most of the birds which were caught put on weight rapidly during rainstorms and appeared to depart immediately after clearing. Immatures appeared to put on weight more slowly than adults.

4. At Drumlin Farm, Massachusetts, many more very heavy birds (16-23 gm.) were caught. In at least two different years a group of birds of average weight 20.8 gm. has been caught in late September and early October, and three such birds have been killed during nocturnal migration at this time. It is suggested that this is the usual departure weight of the species.

5. At Block Island, Rhode Island, a few very heavy birds were caught in both 1959 and 1960, but most birds caught were light immatures (9-12 gm.), most of which arrived very late in the season.

6. New England is an area where Blackpoll Warblers pause in their migration for several weeks to put on fat for overseas flight.

7. Arrivals and departures of Blackpoll Warblers, detected by banding at Round Hill, coincided with movements observed by radar in directions between south and southeast, but not with south-westward movements.

8. On the night of 2-3 October 1962, many heavy Blackpoll Warblers (average weight 17.3 gm.) were attracted to the Bermuda lighthouse: these birds were part of a flight from New England which passed Bermuda without stopping. Lighter birds (11-16 gm.) stopped on Bermuda on several days later in October, but these birds had not flown directly from New England.

9. Forty-five birds kept overnight in dark cages lost weight at an average rate of 0.062 gm./hour.

10. The birds which flew to Bermuda during 1-3 October 1962 lost weight at an average rate of 0.107 ± 0.013 gm./hour; this figure may be an over-estimate but is unlikely to be an under-estimate. This gives an upper limit for their average power consumption of 1.02 ± 0.13 Kcal./hour, only about 2.0 times the resting power consumption in spite of a load of 6-10 gm. of fat. It is argued that they lost little or no water during the flight, but this needs further study.

11. Blackpoll Warblers have sufficient fuel-reserves when they leave New England to fly non-stop for 105-115 hours. This is enough for a non-stop flight to the mainland of South America in the usual weather in which they migrate.

PART II

1. Eight field-studies of migrating birds are summarized, and an estimate of the rate of weight-loss obtained from each. Except for two doubtful estimates, all the figures lie between 0.56 percent and 1.3 percent of total body-weight per hour; the estimate for the Blackpoll Warbler is the lowest and probably the most reliable. It is suggested that a reasonable average for the power consumption of migrating passerines is 0.076 Kcal./gm. total weight/hour: this figure will be too high if some of the observed weight-loss consists of water.

2. A laboratory measurement of the power consumption of a hovering hummingbird was 0.206 Kcal./gm. total weight/hour, which is 2.7 times that suggested for passerines in forward flight.

3. Nine theoretical calculations of the power consumption of flying birds are reviewed. Their predictions range from far below the lowest field-estimate to far above the highest. The most reliable estimates are those from semi-empirical theories based on the measurements of hummingbirds. Aerodynamic theories are at

present unsatisfactory, but at least one offers promise for future development. Physiological theories suggest that some very fat birds expend power at a rate approaching the maximum possible for the organism. Physiological and aerodynamic theories which agree for small birds diverge for large birds, and the discrepancy should be tested by experiments on large birds.

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LITERATURE CITED

- ALLEN, G. M. 1903. *A List of the Birds of New Hampshire*. Manchester, N. H.
- BAGG, A. M. 1950. Reverse warbler migration in the Connecticut valley. *Auk*, **67**: 244-245.
- BAGG, A. M. and EMERY, R. P. 1961. Northeast Maritime Region. *Audubon Field Notes*, **15**: 10-17.
- BAIRD, J., BAGG, A. M., NISBET, I. C. T. and ROBBINS, C. S. 1959. Operation Recovery—report on mist-netting along the Atlantic coast in 1958. *Bird-Banding*, **30**: 143-171.
- BAIRD, J. and NISBET, I. C. T. 1960. Northward fall migration on the Atlantic coast and its relation to offshore drift. *Auk*, **77**: 119-149.

- BISHOP, L. B. 1905. The direction of flight in the fall migration at New Haven, Connecticut. *Auk*, **22**: 372-378.
- BOEL, M. 1929. Scientific studies of natural flight. *Trans. Amer. Soc. Mech. Eng.*, **51**: 217-242. (Notread: quoted by Brown 1961b).
- BROWN, R. H. J. 1961a. Flight. Chapter 20 in A. J. Marshall's *Biology and Comparative Physiology of Birds*. Vol. 2. New York.
- 1961b. The power requirements of birds in flight. *Symp. Zool. Soc. London*, **5**: 95-99.
- BROWNE, K. and BROWNE, E. 1956. An analysis of the weights of birds trapped on Skokholm. *Brit. Birds*, **49**: 241-257.
- BUTTERFIELD, W. A. 1952. A statistical note on bird weights from Lista (Norway) and Fair Isle. *Bull. Fair Isle Bird Obs.*, **1**(6): 30-31.
- CONNELL, C. E., ODUM, E. P. and KALE, H. Fat-free weights of birds. *Auk*, **77**: 1-9.
- COOKE, W. W. 1915. Bird Migration. *U. S. Dept. Agriculture Bull.* 185. Washington, D. C.
- DAVIS, P. 1962. Robin recaptures on Fair Isle. *Brit. Birds*, **55**: 225-229.
- DENNIS, J. V. and WHITTLES, L. J. 1955. The riddle of fall migration at Nantucket. *Bull. Mass. Audubon Soc.*, **40**: 357-366.
- DRURY, W. H. and KEITH, J. A. 1962. Radar studies of songbird migration in eastern New England. *Ibis*, **104**: 449-489.
- ELIASSEN, E. 1963. Preliminary results from new methods of investigating the physiology of birds during flight. *Ibis*, **105**: 234-237.
- ELIASSEN, E. and HJELMTVEDT, I. 1958. The loss of water in wind-drifted migratory birds. *Univ. Bergen Arbok, Naturv. rekke*, **11**.
- GRABER, R. R. and GRABER, J. W. 1962. Weight characteristics of birds killed in nocturnal migration. *Wilson Bull.*, **74**: 74-88.
- GREENEWALT, C. H. 1960a. The wings of birds and insects as mechanical oscillators. *Proc. Am. Phil. Soc.*, **104**: 605-611.
- 1960b. Dimensional relationships for flying animals. Greenville, Delaware: privately printed. Republished as *Smithsonian Misc. Coll.*, **144**, no. 2, 1962.
- 1960c. *Hummingbirds*. New York.
- GRISCOM, L. and SNYDER, D. E. 1955. *The Birds of Massachusetts*. Salem.
- GROEBBELS, F., KIRCHNER, H. and MOEBERT, F. 1938. *Ornithologische Hilfstabellen*. Berlin.
- HELMS, C. W. 1959. Song and Tree Sparrow weight and fat before and after a night of migration. *Wilson Bull.*, **71**: 244-253.
- HELMS, C. W. and DRURY, W. H. 1960. Winter and migratory weight and fat: field studies on some North American buntings. *Bird-Banding*, **31**: 1-40.
- HOLST, E. VON and KÜCHEMANN, D. 1942. Biological and aerodynamic problems of animal flight. *J. Roy. Aero. Soc.*, **46**: 39-56.
- HYATT, J. H. and MYLNE, C. K. 1952. Ornithological observations at Lista 1951. *Stavanger Mus. Opusc. Ser. Zool. (Sterna)*, **7**. Stavanger.
- JENKINS, D. 1953. Migration in late September and early October, 1951. *Brit. Birds*, **46**: 77-98, 121-131.
- KENDEIGH, S. C. 1944. Effect of air temperature on the rate of energy metabolism in the English Sparrow. *J. Exp. Zool.*, **96**: 1-16.
- KING, J. R. and FARNER, D. S. 1961. Energy metabolism, thermoregulation, and body temperature. Chapter 19 in A. J. Marshall's *Biology and Comparative Physiology of Birds*. Vol. 2. New York.
- LACK, D. 1959. Migration over the sea. *Ibis*, **101**: 374-399.
- 1960. Autumn "drift-migration" on the English east coast. *Brit. Birds*, **53**: 325-352, 379-397.
- LASIEWSKI, R. C. 1962. The energetics of migrating hummingbirds. *Condor*, **64**: 324.
- MEINERTZHAGEN, R. 1955. The speed and altitude of bird flight (with notes on other animals). *Ibis*, **97**: 81-117.

- NISBET, I. C. T. 1957. Passerine migration in south Scandinavia in the autumn of 1954. *Ibis*, **99**: 228-268.
- 1963a. Observations with radar of the height of nocturnal migration over Cape Cod, Massachusetts. *Bird-Banding*, **34**: 57-67.
- 1963b. Quantitative study of migration with 23-centimetre radar. *Ibis*, **105**:
- NORRIS, R. A. 1961. A modification of the Miller method of aging live passerine birds. *Bird-Banding*, **32**: 55-59.
- ODUM, E. P. 1945. The heart-rate of small birds. *Science*, **101**: 153-154.
- 1960. Lipid levels in nocturnal migrant birds. *Proc. XII Int. Orn. Congr.:* 563-576.
- , CONNELL, C. E. and STODDARD, H. L. 1961. Flight energy and estimated flight ranges of some migratory birds. *Auk*, **78**: 515-527.
- PEARSON, O. P. 1950. The metabolism of hummingbirds. *Condor*, **52**: 145-152.
- 1954. The daily energy requirements of a wild Anna Hummingbird. *Condor*, **56**: 317-322.
- RASPET, G. 1950. Performance measurements of soaring bird. *Gliding*, **6**: 145-151.
- SALT, G. W. and ZEUTHEN, E. 1960. The respiratory system. Chapter 10 in A. J. Marshall's *Biology and Comparative Physiology of Birds*. Vol. 1. New York.
- SEIBERT, H. C. 1949. Differences between migrant and nonmigrant birds in food and water intake at various temperatures and photoperiods. *Auk*, **66**: 128-153.
- VOOUS, K. H. 1953. Vogeltrek op de Nederlandse Benedenwindse Eilanden. *West Indische Gids*, **33**: 183-190.
- 1957. The birds of Aruba, Curaçao and Bonaire. Vol VII of *Studies on the Fauna of Curaçao and other Caribbean Islands*. The Hague.
- WALKER, G. T. 1925. The flapping flight of birds. *J. Roy. Aero. Soc.*, **29**: 590-594.
- 1927. The flapping flight of birds. II. *J. Roy. Aero. Soc.*, **31**: 337-342.
- WEISS-FOGH, T. 1961. The flapping flight of animals. Harvard Prather Lecture Series (unpublished).
- WETMORE, A. 1939. Observations on the birds of northern Venezuela. *Proc. U. S. Nat. Mus.*, **87**: 173-260.
- WILKIE, D. R. 1959. The work output of animals: flight by birds and by man-power. *Nature*, **183**: 1515-1516.
- WILLIAMSON, K. 1952. Migrational drift in Britain in autumn 1951. *Scot. Nat.*, **64**: 1-18.
- 1958. Bergmann's rule and obligatory overseas migration. *Brit. Birds*, **51**: 209-232.
- 1961. The concept of 'cyclonic approach'. *Bird Migration*, **1**: 235-239.
- YAPP, W. B. 1956. Two physiological considerations in bird migration. *Wilson Bull.*, **68**: 312-319.
- 1962. Some physical limitations on migration. *Ibis*, **104**: 86-89.
- ZEUTHEN, E. 1942. The ventilation of the respiratory tract in birds. *Kgl. Danske. Videnskab. Selskab Biol. Medd.*, **17**: 1-50.