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## ENERGY METABOLISM AND THEORETICAL FLIGHT RANGE OF BIRDS

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*Part I Estimation of Energy Metabolism of Sustained Flight of Birds*

### INTRODUCTION

In recent years many investigations have shown increased interest in quantitative estimate of the weight loss per unit time and energy metabolism of migratory flight. Theoretical estimates of the per cent body weight loss per hour ranged from as high as 12.5 per cent (Zeuthen, 1942; Salt and Zeuthen, 1960) to as low as 0.4 per cent (Yapp, 1956, 1962). Many estimates based on empirical data now available on weights of departing and arriving migrants have been compiled (*cf.* Nisbet, 1963 for review). Several authors have advanced theoretical computations on the energy expenditure of flight in birds (Brown, 1961; Nisbet *et al.*, 1963; Raspel, 1960; Wilkie, 1959; Yapp, 1956, 1962; and Zeuthen, 1942); others have derived various indirect estimates for determining flight metabolism in birds (Lasiewski, 1962, 1963; LeFebvre, 1964; Odum, 1960; Pearson, 1950, 1964).

Nisbet (1963) has contributed an excellent review of the field estimates and theories available. He pointed out that there are weaknesses or obvious errors in prior estimates and theories, and he recalculated many original field data to derive revised estimates of weight loss per hour of flight. One of the major conclusions of that review was that other available field estimates and theories lent support to the conclusion of Nisbet (1963) that the average power consumption in small birds is about 0.076 kcal/gm total weight/hr or is about twice the resting metabolism. This conclusion was based upon the rate of weight loss calculated for many species from data available in the literature. The individual field estimate considered by Nisbet (1963) to be most reliable was that of Nisbet *et al.* (1963) for the Blackpoll Warbler (*Dendroica striata*); this estimate was also the lowest and contributed to lowering the average suggested by Nisbet (1963).

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We believe that the estimate of weight loss per hour of flight (0.56% total weight/hour) and therefore the corresponding estimate of energy metabolism of flight by Nisbet *et al.* (1963) is low for small (10-30 gm) migrating passerines. We present a method for estimating the energy metabolism of flight which we believe yields equally reasonable estimates and is applicable for a wider range of species.

#### ESTIMATING FLIGHT ENERGY CONSUMPTION

The proposed method for estimating the flight energy expenditure in birds is simply to assume that normal steady flight is sustained hard work which requires an energy expenditure that is some multiple of standard or resting energy metabolism. The use of such ratios has been substantiated to some degree for birds in previous studies (*cf.* Lasiewski, 1963; LeFebvre, 1964:412-413; Odum, 1960; Pearson, 1950, 1954).

The ratios and the basis for them are provided in part by Brody's (1945:916) investigation of the work capacities of large domestic animals; he concluded that sustained hard work required eight times the *resting* energy requirements or twelve times the basal energy requirements in man and horse and that such ratios were probably independent of size or species.

The term resting metabolism is used frequently and in diverse enough meaning to warrant some elaboration on our usage and the precise meaning Brody meant to convey. It was defined at least twice by Brody (1945:59 and 352) as basal or standard metabolism plus the specific dynamic action (SDA) of the diet. He further stated SDA is about 50 per cent in cattle. The curves relating work energy expenditures to basal and resting energy levels (1945:916) give a basal to resting ratio of 12/8 or 1.5:1; again providing a resting energy value of 50 per cent above basal.

While Brody was careful to designate resting and basal energy (or oxygen consumption) on his graphs, he was more vague in the text. Thus he stated (1945:915) that Dill (1936) obtained a sustained hard work/basal energy ratio of 3-8, and he noted a hard work/basal energy ratio of 8 for a 1500 pound horse working 8 hours per day at 1 horse power. But in discussing Dill's results, Brody pointed out that *during hard work proper the hard work to rest ratio was 8*; thus he concluded on page 917 that oxygen consumption of sustained heavy-work was 3-8 fold *rest*. The contradictory statements resulted because both Dill and Brody were interested in practical problems, and they measured hard work energy requirements in horse and man working a regular 8-10 hour work day. We wish to know the ratio of energy requirements of sustained hard work *when working* to resting or basal rates. Brody (1945:916) showed graphically that a 1500 pound horse working hard for 24 hours used 120,000 kcal (1 1/2 HP) which is 12 times the basal rate or 8 times the resting rate. This latter figure which is 15,000 kcal/24 hours compares favorably to the resting energy consumption for a 1500 pound horse determined

directly (Brody 1945:422). The ratio of 8 for hard work to rest corresponds to Dill's (1936) ratio for man while working (not compared on a 24 hour basis). Thus, from Brody's findings and the collaborative evidence, energy expenditure for various activity levels may be estimated by using the following ratios: resting is 1.5 basal; moderate work is 3-8 basal; sustained hard work is 12 basal; maximal work (Brody, 1945:915-918) or peak-effort is 100 fold basal. In addition to the avian studies cited (Lasiewski, 1963; LeFebvre, 1964; Odum, 1960; Pearson, 1950, 1954), justification for assuming that the energy metabolism of sustained hard work is expressible as some multiple of standard metabolism is provided by the discussions of Hemmingsen (1960:64-68) and Wilkie (1959).

As Odum (1960) stated, migration must be strenuous but not exhausting; it is a work level that can be maintained until the energy reserve is depleted. Hence a bird migrating, a horse working all day, a runner or hiker keeping up a sustained pace all day should have similar energy requirements relative to the basal (and resting) level.

Actually we are not proposing a radically new method of flight energy calculation but modifying the technique used by Odum (1960). Odum (1960) estimated flight energy requirements in small passerine birds as six times the basal energy consumption. He used Pearson's (1950) resting oxygen consumptions as basal values in justifying the method of calculation. Fortunately Pearson's values were actually closer to resting energy levels than to basal levels and thereby somewhat fortuitously provided Odum with reasonable estimates.

#### APPLICATION OF METHOD

To make an estimate of energy metabolism one may begin by either measuring directly standard or resting metabolism or calculating this parameter by use of an appropriate equation. Sufficient empirical data are available to permit a confident estimate of the standard metabolism using the equation provided by King and Farner (1961:230, equation 6)

$$\log M = \log 74.3 + 0.744 \log \text{wt} \pm 0.074 \text{ (for kcal/day)}$$
$$\text{(or } \log M = \log 3.1 + 0.744 \log \text{wt} \pm 0.074, \text{ for kcal/hr)}$$

For our purposes we have chosen to ignore a slightly different equation for smaller birds (less than 0.1 kg; King and Farner, 1961: 231, equation 7) because the paucity of reliable data for very small birds does not allow a clear choice of which equation best represents their metabolic activity. It can be shown that very small mammals do not deviate from the linear model (*cf.* Kleiber, 1947, 1950 and King and Farner, 1961) and the standard metabolic rates obtained by Lasiewski (1963) agree favorably with values one would obtain by use of the above equation. Until there is more conclusive experimental evidence to the contrary, we shall assume the general equation (*i.e.* 6) best represents the standard metabolic rate of birds, regardless of size (*cf.* Lasiewski, 1964:216).

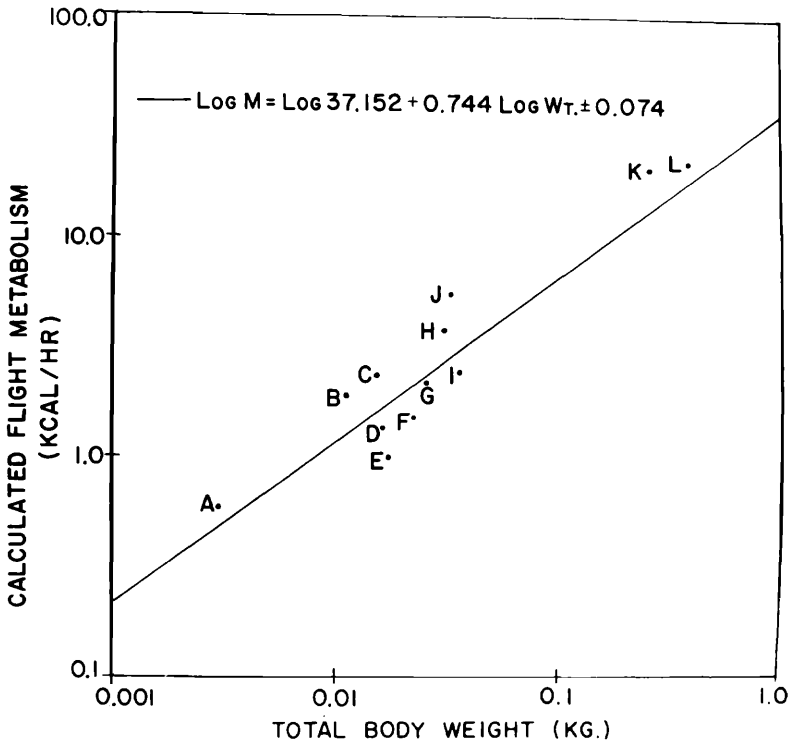


Figure 1. Comparison of various empirical data with theoretical curve for flight energy metabolism in birds. Solid line is twelve times the standard metabolism curve (in kcal/hr) from King and Farner (1960: 230).

After obtaining either a direct measurement or a calculation of the standard metabolic rate, the total flight energy expenditure is obtained by multiplying by twelve. This value is the total energy expended by the bird during flight and does not represent the "work output" of flight.

#### COMPARISON WITH OTHER ESTIMATES

To test the validity of our method of estimate, comparisons are made in Figure 1 with other empirically, and two semi-empirically, derived estimates of flight metabolism. The solid diagonal curve represents the calculated flight energy metabolism as a function of body weight (as twelve times the standard metabolism rate in kcal/hr) and the points plotted represent various other estimates or empirical findings:

(a) Point a represents the plot of the total energy expenditure associated with hovering flight in the Costa's hummingbird, *Calypte costae*, as determined by Lasiewski (1963). He measured an average oxygen consumption of 42.4 cc O<sub>2</sub>/hr for a 35 minute interval of continuous flight. At a caloric equivalent of 0.0047 kcal/ccO<sub>2</sub> and for a mean weight of 3.0 gm the energy consumption is 0.60 kcal/hr. Lasiewski's data are of particular interest to us because of the empirical data we will use in this comparison, only Lasiewski provides a basal or standard metabolic rate determined empirically using the same technique, species, and investigator. Lasiewski's (1963:124, Table 1) values for the minimal levels of metabolism at thermal neutrality for *C. costae* range from 2.8-3.3 ccO<sub>2</sub>/gm-hr for birds weighing 2.9-3.4 gms. The average weight and metabolic rate is respectively 3.2 gm and 3.0 cc O<sub>2</sub>/gm hr. The caloric equivalent per bird is 0.05 kcal/hr. This is 1/12 the energy metabolism of flight determined for the species by Lasiewski. It is interesting to note that if we had only Lasiewski's basal metabolic measurement for this species, our method would predict the identical flight energy expenditure.

(b) Point b represents a field estimate presented for the first time in this paper. The estimate is based on estimated weight loss per hour of flight for Tennessee Warblers (*Vermivora peregrina*) killed at the Eau Claire, Wisconsin television tower during a night of migration on 2-3 October, 1962. Some of the most valuable data from the TV tower-killed birds has been weight data and data on the times, intensities and conditions of migration. This information permits one to estimate weight loss during flight provided some assumptions can be made. The estimated weight loss is calculated from difference in mean weight for samples of birds killed at various time intervals throughout the "kill" period. The necessary assumptions are: (a) that the birds collected for each time interval represent those killed for that period; (b) that the sex and age composition is comparable for each sample or no significant weight differences exist among these classes; (c) that the weight data are equally precise for each sample period; (d) that for any night's kill the entire population began its migratory flight at approximately the same time, hence birds passing one geographical point along the route of the migration in successive time periods have been flying correspondingly longer; and (e) that the passage of birds is essentially linear past the point represented by the tower, or if circling of the tower occurs, the energy cost of flying around this point in space is no greater than regular migratory flight. The first three assumptions are valid when care is taken in collecting the required specimens and data. Assumptions d and e are not subject to validation with present methodology but have been accepted in this report (also see Graber and Graber, 1962).

Estimated weight loss per hour of flight was obtained on a sample of 38 Tennessee Warblers killed from 2130 hours, 2 October to 0300 hours, 3 October 1962. Eighteen specimens killed before 2400 hours were collected at 15 to 30 minute intervals; 20 speci-

mens killed after 2400 hours were collected at dawn. The median time of kill before midnight, based on the number of birds killed for each time period, was 2210 hours. The mean rate of kill averaged 7.6 birds per hour. Extending this rate, the kill of the 20 post midnight specimens lasted about 2.6 hours or until 0230 hours. This agrees closely with Dr. C. A. Kemper's observation (personal communication) that weather conditions which result in the kill conditions (*cf.* Cochran and Graber, 1958; Graber and Cochran, 1960; or Graber and Graber, 1962) changed between 0200 and 0300 hours. Therefore the median time of kill after 2400 hours was estimated to be 0120 hours. The difference in median time between the two samples therefore is approximately three hours. The mean weight of the specimens killed before midnight was  $11.23 \pm 0.24$  (S. E.) gm; the mean weight of those killed after midnight was  $10.62 \pm 0.19$  (S. E.) gm. This difference (0.61 gm) is significant ( $t = 2.00$ , 36 df.,  $p < 0.06$ ) and represents a rate of weight loss of 0.2 gm/hr or 1.83 per cent of the mean weight per hour of flight. If we assume total weight loss represented only fat depletion (following Odum *et al.* 1964), these data provide an estimated total metabolism of flight of 1.90 kcal/hr. The sex class composition (the only category having a significant difference in fat-free weight; see Part II) was essentially equal; males constituted 55 and 60 per cent, respectively, of the pre- and post-midnight samples.

(c) Nisbet (1963:146) developed a new theory on the basis of water retention, adapting Salt and Zeuthen's (1960) calculations and Kendeigh's (1944) data to yield an estimate of maximum possible rate of energy utilization. Above this consumption, water loss would prevent long distance migration. Nisbet obtained values of 2.61 kcal/hr and 2.09 kcal/hr as the maximum energy consumption for a 10 gm lean bird and 20 gm fat bird (10 gm of fat) respectively. Point c represents an average value of 2.35 kcal/hr for a 15 gm bird.

(d) Point d represents the metabolic rate of flight for the European Robin (*Erithacus rubecula*) based on the estimated rate of weight loss ( $0.88 \pm 0.15$  per cent mean wt) calculated by Nisbet (1963:139) from the data of Butterfield (1952) and Davis (1962). Using a mean weight of 16.3 gm for the sample discussed and converting to energy expenditure, this is 1.36 kcal/hr.

(e) Point e represents the estimation of energy consumption for Blackpoll Warblers (*Dendroica striata*) of 1.02 kcal/hr provided by Nisbet *et al.* (1963:137). This is the field estimate which Nisbet (1963:156) believed was the most reliable.

(f) Weight data obtained on Song Sparrows (*Melospiza melodia*) by Helms (1959) was reviewed by Nisbet (1963:142). The average weight loss was 1.61 gm/hr which probably occurred during a 10 hr migration. Point f corresponds to the energy expenditure of flight (1.53 kcal/hr) this loss would provide. Nisbet concluded the assumptions involved in this weight loss estimate led to an underestimate.

(g) Odum (1960) suggested that the total energy requirement of flight was between two to four times "existence" energy requirements. For 20-25 gm birds he approximated the "existence" energy requirements as 1 kcal/hr; hence obtaining a flight energy requirement of 2-4 kcal/hr. Subsequently, Odum modified his original estimates following a suggestion of Nisbet to account for changing power requirements as the fat load increased or decreased (Odum *et al.* 1961). In reviewing Odum's estimates Nisbet (1963:147) considered the best estimates from Odum's theory to be 0.075-0.10 kcal/gm total wt/hr. For a 25 gm bird this provides an *average* calculated energy expenditure of 2.20 kcal/hr of flight, represented on our graph at Point g.

(h) Point h represents the field estimate of flight energy metabolism for Greenland Wheatears (*Oenanthe oenanthe*) as provided by the data from Williamson (1958, 1961) and Nisbet (1963:141). Assuming a mean weight of 31.0 gm and a rate of weight loss of 1.3 per cent of the mean weight which is entirely fat loss, the calculated metabolic rate is 3.82 kcal/hr.

(i) Another estimate of flight metabolic rate for Greenland Wheatears was provided by Nisbet (1963:141) utilizing the data from P. Davis (*in litt.*, cited by Nisbet, 1963:141). Point i represents the energy requirements of 2.45 kcal/hr based on a mean weight of 34.5 gm and a rate of weight loss of 0.75 per cent of the mean weight/hr.

(j) Point j represents an additional estimate of flight energy requirements based on a "kill" of Swainson Thrushes (*Hylocichla ustulata*) at a TV tower. Graber and Graber (1962) provided the original data which were recalculated by Nisbet (1963:143) to provide a mean weight loss of 1.8 per cent per hour. For a mean weight of 32 gms the calculated energy expenditure is 5.47 kcal/hr if the entire weight loss is assumed to be fat loss.

(k) Pearson (1964) determined the weight loss in Tippler pigeons flying for periods of 3 to 6.23 hours. His birds lost weight at an average of 3.0 gm/hr of flight. If this is entirely fat, these data indicate for his pigeons (having an average body weight of 0.254 kg) an energy expenditure of flight of 28.5 kcal/hr. It is permissible to estimate water loss in Pearson's birds because water loss data were obtained on this species by LeFebvre (1964). LeFebvre found an algebraic water loss of 7.4 gm and a mean water loss of 10.5 gm for eight birds which flew a total distance of 300 miles in 8.6 hours. This represented 23-33 per cent of the total weight loss in his pigeons. For Pearson's data this would indicate that fat loss was 2.0-2.3 gm/hr. The average energy equivalent would be 20.4 kcal/hr which is plotted at Point k.

(l) Point l is the energy expenditure of flight determined by LeFebvre (1964) on free flying pigeons using the doubly-labeled water ( $D_2O^{18}$ ) method of Lifson *et al.* (1955). This value represents an energy expenditure of 22.0 kcal/hr for pigeons averaging 0.384 kg in weight.

## DISCUSSION

An examination of Figure 1 reveals that there is a reasonable agreement of the empirical plots with our theoretical curve (solid line). Although a number of points deviate rather widely, the data do cluster around the curve. A linear regression (unweighted data;  $\log M = \log 48.98 + 0.799 \log w + 0.048$ ; wt = average total body weight for each point) was computed for the data points in order to test the significance of the difference in slopes between the two curves. No significant difference was found ( $t = 0.618$ , 10 d.f.,  $P > 0.50$ ). However, we realize this comparison provides only moderate confirmation of our theoretical curve because the compared data are derived from three dissimilar sources not amenable to such analysis (theoretical estimates, weight losses of unknown fat and water partitioning, and known fat and water partitioning). Ideally, continued compilation of weight loss estimates in which the fat loss is known will permit a valid statistical comparison when sufficient sample sizes are available.

Specific consideration of individual deviants provides some justification for suggesting that all the empirical data, within the limits of reliability one could place in them, support our method for approximating flight metabolic requirements. It should be noted that only one point (e) is for a metabolic rate greatly less than what we would estimate. To this extent these data at least support our proposed method of estimation involving a multiple of 12 fold standard or 8 fold resting metabolism rather than lower ratios as has been suggested (Nisbet *et al.* 1963; Yapp, 1956, 1962).

We cannot readily account for the unusually low estimate for flight energy expenditure by Nisbet *et al.* (1963). We agree that the field work and radar observations reported justify their estimate, however, these data are not necessarily more reliable than other field estimates nor do they unequivocally support the estimate provided (see also Murray, 1965).

Nisbet *et al.* (1963) have inherent in their calculations the same assumptions true of other estimates based on comparisons of departure weight with arrival-weights at another locality. Their estimate is totally dependent upon the weights of just 14 Blackpolls caught at a lighthouse on Bermuda which the authors felt must have been part of a flight that left New England 32 hours earlier. Even with radar and prior searching on Bermuda this assumption may be invalid. It is interesting to note that all other samples of Blackpolls subsequently caught at Bermuda were considerably lighter than the 14 used by Nisbet *et al.* (1963). These subsequent data were dismissed because radar suggested that these birds could not have flown directly over New England.

One of the most obvious explanations for such unusually low values is that one of the assumptions involved may not be valid. Particularly we suggest that the length of time for the migration from New England to Bermuda may have been overestimated. Graber and Hassler (1962) found in their radar study that the usual ground speeds for small passerine birds were between 34 and 45



mph. Nisbet *et al.* (1963) do not give the value of the ground speed used in their calculation but state, ". . . that the time of arrival agrees exactly with the ground speed of the birds (22 knots airspeed plus a favoring wind of a few knots) . . .". Yet Nisbet *et al.* (1963) used 32 hours, (which may represent a maximum estimate) in their calculation for the flight time to Bermuda (average distance from New England coast, 770 miles) which yields a ground speed of only 24 mph (21 knots). This appears to be too low because their data (Table 7, p. 129) indicate that there were following or near following winds of 10 to 13 knots for birds migrating on October 1-2 and 2-3; thus providing a ground speed of 32 knots or 36.9 mph. This value provides a probable minimum flight time of 20.9 hours with a weight loss of 0.164 gm/hr or 0.86 per cent of the mean body weight per hour. The kilocaloric equivalent, assuming fat katabolism, is 1.56 kcal/hr. This rate of expenditure, while still low, is more compatible to our predicted value (Fig. 1).

The Blackpoll Warbler has a great propensity for storing migratory fat. Nisbet *et al.* (1963) concluded that the Blackpoll has progressed strikingly as an efficient long distance migrant. It is indeed tenable that selection resulted in adaptation in this species for long overwater flights. Such adaptations could include a higher efficiency of work output requiring a lesser total metabolic effort, but we would anticipate instead, an adaptation toward increased fat depots as more probable.

The data plotted at b, c, h, j, and k fall rather wide above our theoretical estimate. Points b, h and j are based on the assumption that the entire weight loss is fat loss whereas this may not be true. As water loss occurs these points would move closer to our curve. That water loss would occur appears probable, especially for the Swainson Thrush (j), for it is unlikely that this species, not particularly noted as a strong long distance migrant, should have evolved the water conserving adaptation which is suggested for the Blackpoll Warbler by the data and discussion of Nisbet *et al.* (1963:136). Data Point c is a maximum estimate of metabolism and need not nullify our suggestion because energy expenditure required in the assumptions may be more characteristic of maximal exertion rather than *sustained* effort. We can suggest no reason at this time for the disagreement between the rate predicted by our curve and the empirical results (k) obtained by Pearson (1964). Indeed if our adjustment for water loss for these pigeons is invalid, point k might deviate further from our predicted value.

As stated earlier, our basic assumption is that flight (for most birds) is sustained hard work and can be expressed as a multiple of the standard metabolism. This agrees with Wilkie's (1959) conclusion that the work output of animals varies with size as does the resting metabolism, and the maximum effort possible is related to the standard (or resting) metabolic rate. While providing only an approximate estimation of total metabolic expenditure during flight, this approach should be of heuristic value. The generalization suggests a basic physiologic mechanism limiting sustained energy expenditure in homoiotherms.

The validity of the assumptions and the method of estimation is enhanced as empirical data tend to confirm the predicted values for several species of birds. It must be recognized that activity, even flight, if not representative of sustained hard work, would not require the energy expenditure predicted. Hence some species of birds, e.g., soaring hawks, terns and albatrosses, which undoubtedly obtain a considerable degree of energy from work done by the environment would not be expected to fit the theoretical curve proposed in this paper.

## *Part II. Hypothetical Migratory Pattern for Tennessee Warblers*

### INTRODUCTION

Ornithologists have focused increased attention on weight loss and fat reserves in birds as an aid to understanding patterns and extent of migration. Coupled with the basic interest in this area is an awareness of the applied importance of this knowledge as birds are increasingly implicated as factors in the spread of fungal and viral diseases of plants and animals. Extended knowledge for many species will be desired in the future. Specific knowledge on movements and migratory patterns and capabilities will be attained for many species by a jig saw puzzle process of piecing together information on breeding and wintering areas, energetic requirements of flight, energy reserves, and flight capabilities of particular species. Much of this information is already available, much must be assessed or surmised.

In the preceding section we proposed a method for approximating one of the parameters necessary to understand the total migratory pattern for a species. The approach provides a ready means for calculating the total metabolic requirements for steady flight which, for one reason or another, cannot conveniently be determined directly. In this section, the intent is to utilize that parameter to construct a, admittedly speculative, fall migratory pattern for a population of Tennessee Warblers (*Vermivora peregrina*) killed during nocturnal migration at the Eau Claire, Wisconsin TV tower. To develop our hypothetical pattern, we require information on: (1) the rate of energy expenditure during flight, (2) the minimum energy reserve maintained during the migration, (3) the mean weight of the migrating population, and (4) the mean time of the migratory flight past the tower site.

The predicted value from the theoretical curve in Figure 1 for our estimate of energy expenditure of flight is 1.3 kcal/hr. We shall use this value in developing our hypothetical pattern even though we have field data providing an energy expenditure of 1.9 kcal/hr from which an alternative pattern could be derived. Our purpose is to use the predicted value for approximating the expenditure parameter in order to deduce certain aspects of migrational behavior. It is implicit in our reasoning that, for many problems, the theoretical curve provides a basis for such deductions that at this time is as reliable as isolated field estimations. These, in themselves, are often approximations or, of necessity, require

assumptions in their derivation; hence when a field study is not applicable we suggest the theoretical approximation may justifiably be utilized.

To obtain the minimum energy reserves normally maintained during migratory flight we first obtained the fat-free weight for this species. Connell *et al.* (1960) have demonstrated that in birds, the fat-free weight for a given species and sex is a very constant figure. This is especially true for fat-free weights of individuals having the same wing length. For the Tennessee Warbler they reported a fat-free weight of  $7.94 \pm 0.13$  (S.E.) gm, but these data were based on only eleven specimens which included both sexes.

Because of the small sample size, we determined the lipid content for 49 Tennessee Warblers. All age-sex classes were represented in this sample. Lipid content was defined as the extractable residue determined by diethyl-ether extraction in a soxhlet apparatus on dehydrated, ground-up carcasses. Extraction was continued for 24 hours or more. The extract was evaporated until only the non-volatile residue remained. The results showed no significant difference in fat-free weight between the adults and immatures within either sex class, but there was a significant difference in fat-free weight between the sexes. For males and females respectively ( $n = 19$  and  $30$ ) the fat-free weight was  $8.39 \pm 0.09$  (S.E.) gm and  $8.02 \pm 0.06$  (S.E.) gm. Odum (1960) suggested that at least a small portion of the fat reserves be considered unavailable (structural lipids) for energy expenditure in calculating flight ranges. Following this suggestion, we will consider the minimum energy reserve to be 8.5 gm (mean fat-free weight plus 0.3 gm non-expendable lipids).

#### THEORETICAL MIGRATORY PATTERN

Having established for the Tennessee Warbler the rate of energy expenditure and the maximum allowable depletion of energy reserve, one can readily calculate from the actual mean weight for the sample at the time of collection, the potential flight range for birds interrupted in their migration. Such projections for total potential range have been made (e.g., Caldwell *et al.*, 1963; Lasiewski, 1963; Odum, 1960; Odum *et al.*, 1961). Equally logical back projections can be made to estimate origins of a migratory flight, thus permitting construction of a migratory pattern which would become more meaningful as data from TV tower kills, radar studies, banding and field observations continue to amass. Such a construct would be applicable to any time-sample during the migration provided the sample was sufficient to provide a reliable estimate of the population mean weight. For simplicity, we will use for our example the sample of 38 birds collected on 2-3 October, 1962. This seems reasonable in this case because the rate of kill throughout this evening appears to be uniform and we can establish the median time of kill at 2400 hours. The mean weight for the entire sample is  $10.91 \pm 0.16$  (S.E.) gm. For our calcu-

lations we shall assume the average ground speed to be 40 mph *cf.* Graber and Hassler, 1962). Available fat was calculated as the total mean wet-weight less the minimum energy reserve of 8.5 gm. For our estimate of energy expenditure of 1.30 kcal/hr the fat loss equivalent is 0.14 gm/hr. Hence, for this sample, the potential flight range beyond Eau Claire would be about  $690 \pm 45$  miles =  $(2.41 \pm 0.16 \text{ gm available fat} \times 40 \text{ mph})$ .

$$0.14 \text{ gm/hr}$$

To postulate the probable area of origin (both proximal and ultimate) for the Tennessee Warblers killed at Eau Claire, further assumptions are required. These include the supposition that: (a) the nocturnal flights originate at dusk and continue for about ten hours (Drury and Keith, 1962); (b) that at the ultimate area of origin this population had an average initial fat load which was approximately 40 per cent of the wet fat-free weight as found by Odum *et al.* (1961); and (c) that the birds interrupt their migration whenever fat reserves are insufficient to provide for a full night's migration or whenever a barrier is reached for which the available fat reserve is not sufficient to complete the necessary flight.

The suggestion by Caldwell *et al.* (1963), favoring a gradual buildup of fat reserves as migration proceeds would exclude our second assumption. However, this proposal should for the present be considered quite tentative and speculative, particularly for individual species, as they present no data on fat buildup *per se*, but only data on fat deposits of birds already in migration. The general pattern evident from Caldwell *et al.* (1963) comparison of fat levels from Michigan and Florida TV tower-killed birds may only reflect the relationship between tower location and different areas of origin of peak weight migrants. For example, Raveling (1965) pointed out that, based on chance alone, most migrants killed at the Eau Claire, Wisconsin TV tower probably originated quite far north or north-west; particularly, all samples of Tennessee Warblers analyzed were probably from the more northern reaches of their breeding range. The same would seem to be true for most species killed at the Michigan site; whereas the unique location of the Florida site reflects kills of birds which have replenished fat stores enabling them to cross the Gulf of Mexico.

It is further assumed that the birds are not otherwise replenishing their fat stores between successive flights but that they may feed enough to compensate for whatever daily existence requirements are needed. It would be inefficient for many species to feed after initial migratory flights, especially if they still had enough available fat to undertake additional long flights. Fall migrations of many passerines would seem to have evolved not only to coincide with favorable weather for migration (Williamson, 1953; Drury and Keith, 1962) and seasonal ecological considerations, especially that of food supply (Lack, 1960), but also with enough reserve energy stored to insure reaching more southerly latitudes where food supply would probably not be a major problem. Insectivorous species, especially more northern populations, might experience

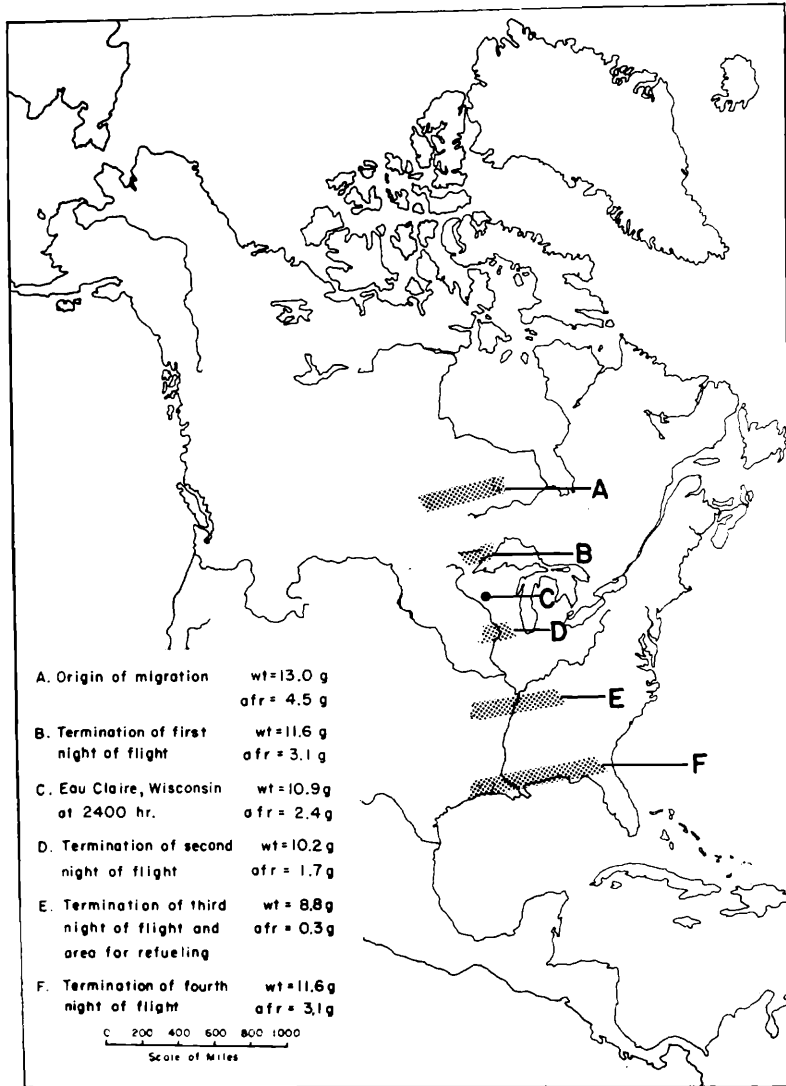


Figure 2. Hypothetical migratory pattern for a sample population of Tennessee Warblers killed at the Eau Claire, Wisconsin TV tower. Wt = weight; afr = available fat reserve.

difficulties finding food in the first stages of migration from the breeding grounds. At times, in periods of poor food supply in intermediate areas, a barrier as effective as the Gulf of Mexico or other long overwater flights would occur if complete reserve replenishment were necessary. Observers in nearly any part of the country can see active feeding fall warblers, but this does not negate the assumption that birds with considerable fat stores still available to them are not actively feeding. Finally, with respect to water balance, we shall assume that a relatively constant per cent body water consumption is maintained during the overland migration. Although water loss may occur during the flight proper, it appears most reasonable to assume opportunity is provided during the day for maintenance of water balance. Hence in establishing our pattern of migration we need account only for a net loss of fat reserves during the nocturnal migration.

Thus, a population of Tennessee Warblers weighing an average of 10.9 gm having an available fat reserve equal to 2.4 gm passing Eau Claire, Wisconsin at 2400 hours (median time of passage for this sample population) would have been migrating for approximately five hours and should continue five hours more. At an average ground speed of 40 mph, their flight originated in an area 200 miles north of Eau Claire, and would terminate 200 miles south (Figure 2). Upon termination of this flight, the birds would be at the latitude of northern Illinois; their body weight would be 10.2 gm (following Odum *et al.* 1964, assuming fat loss = weight loss); their fat reserves would be decreased to 1.7 gm. The fat reserves continue to be sufficient for another 10 hour flight, which would place the population at point E in Figure 2. At this stage however, the fat reserves would be depleted and migration would be interrupted until replenishment is completed. Resuming migration again with an initial weight of 13.0 gm and an available fat reserve of 4.5 gm, the hypothetical Tennessee Warbler population would complete one more night of migration placing them in the Gulf Coast region. The fat reserves would be quite sufficient to complete a continuous long over-water flight under the assumptions stated. Similar calculations permit a "back-tracking" of this population to each night's area of origin or the ultimate area of origin. Figure 2 portrays the hypothetical pattern based on the assumptions presented.

Many variables are involved in the pattern of migration and the theoretical account is of necessity highly simplified. We fully realize the tenuous basis for the particular pattern developed and presented in Figure 2. This pattern can only be suggested provided the number of assumptions which introduced the construct are valid. One might therefore justly question the usefulness of this approach. Nevertheless we should like to urge that this method has heuristic value because it focuses attention on particular assumptions and directs observations to answer particular questions. It provides interesting possibilities in analyzing migrations of birds utilizing the relatively sparse field data we now possess. Such patterns will become more realistic as our knowledge accumulates.

## SUMMARY

### Part I

At present, there exists a considerable amount of empirical and theoretical estimates of weight loss and energy expenditure of migratory flight, which Nisbet (1963) has excellently reviewed. He noted the weaknesses inherent in many prior estimates and concluded that power consumption in small birds is about 0.076 kcal/gm total weight/hr. This conclusion, based primarily on calculated weight loss for a small sample of Blackpoll Warblers appears low, in our opinion, for small migrating passerines. We propose, instead, a simple method for estimating flight energy requirements which we believe yields more reasonable results for a wider range of species. Our method proposes that the energy expenditure of sustained flight can be estimated for many species as twelve times the *standard* metabolism rate. Comparison of the predicted estimates and available empirical data provides reasonable support for our method of estimation. A discussion of these data and our curve is presented along with some comments on the estimate provided by Nisbet *et al.* (1963).

### Part II

This section provides a hypothetical construct of a migratory pattern applicable to a sample population of Tennessee Warblers collected at the Eau Claire, Wisconsin TV tower site. Information necessary to develop our construct included the estimation of energy expenditure or weight loss during flight which was predicted from the theoretical curve in part I, the minimum energy storage maintained during the migration, and the mean weight and time of passage for the sample population. The minimum energy storage was obtained from data on fat-free weights of 19 males and 30 females collected at the site. With these data the probable areas of origin and termination of flights permitted derivation of the hypothetical pattern of migration. Admittedly, the pattern is crude, because many assumptions are involved, but similar constructs will become refined and more accurate as data accrue.

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#### ATTENTION CARDINAL BANDERS

As part of an extensive research program being conducted by members of the Department of Zoology, University of Western Ontario, the writers are presently involved with a study of mortality and dispersal of the Cardinal (*Richmondia cardinalis*). IBM punchedcard data, supplied by the Bird Banding Laboratory, are being used for computer analysis. We would appreciate hearing from any one preferring that his recoveries or returns of cardinals be excluded from this study.—Douglas D. Dow, and D. M. Scott, Department of Zoology, University of Western Ontario, London, Canada.