THE MECHANICS OF BIRD MIGRATION

C. J. PENNYCUICK

INTRODUCTION

The accumulation of fat reserves before migration has been much studied, and several authors have considered the problem of predicting how far a migrant bird should be able to fly on a given amount of fuel (Odum, Connell & Stoddard 1961, Yapp 1962, Lasiewski 1962, Nisbet 1963, Raveling & LeFebvre 1967). All have recognized that this depends both on the speed at which the bird flies and on the rate at which it uses up fuel. Whilst speeds can be measured by radar and other methods, it has usually been necessary to estimate the rate of energy consumption from indirect metabolic considerations, the relevance of which is difficult to establish.

The most direct way to determine the energy consumption of a bird flying at a known speed is to measure its oxygen consumption while it is flying steadily in a wind tunnel. This has been achieved by Tucker (1968) with the Budgerigar *Melopsittacus undulatus*, and no doubt further data of this type will be forthcoming. An alternative method, also based on wind tunnel studies, is to estimate the mechanical power required for flight at various speeds from mechanical measurements; the work done in flight, being derived from chemical energy, can then be accounted for in terms of fuel and oxygen consumed. This approach, being based on general mechanical principles, more readily permits the application of particular experimental results to the analysis of animal flight in general.

The basis of such a theoretical approach is the calculation of a curve relating mechanical power required to forward speed. The theory developed by Pennycuick (1968 b) for the pigeon *Columba livia* is here generalized and simplified, and its implications in regard to the speed, height and range of migration in different flying animals are examined. The conclusions are presented in the form of formulae and graphs, which it is hoped will prove useful for estimating the performance of particular animals, and provision has been made for new information to be incorporated as it becomes available, to improve the accuracy of estimates. It is hoped that this will also serve to direct attention to points on which more information is needed. The steps involved in making practical performance estimates are summarized in the Appendix.

METHOD OF ANALYSIS

For reasons which will be explained in the next two sections, the curve of power required in relation to forward speed is necessarily U-shaped, that is, there is a definite speed (V_{mp}) at which the power required is a minimum. Flying either faster or slower than V_{mp} is more strenuous than flying at this *minimum-power speed*. V_{mp} is the speed at which fuel is used most slowly, and it is therefore the speed at which the bird should fly if its object is to remain airborne for as long as possible without feeding.

V_{mp} is *not* the speed at which the bird covers the most distance for a given amount of fuel. This *maximum-range speed* (V_{mr}) is higher than V_{mp}.

The first objective of the performance analysis is to locate the two critical speeds V_{mp} and V_{mr}, and to estimate the power required to fly at these speeds. This is done first for an " ideal bird ", and the argument is then modified to approximate to a real bird. First of all, the power requirements have to be analysed into various components.

ANALYSIS OF POWER REQUIREMENTS

A flying bird expends mechanical power in three main ways:

(1) *Induced power*

To remain airborne the bird must balance its weight by continuously accelerating air downwards, the upward reaction on the wing being equal to the *rate* at which downward momentum is imparted to the air. The power required to impart this downward momentum to the air is called the *induced power* P_i.

The classical theory of induced power is explained in aeronautical textbooks (e.g. von Mises 1945, Shapiro 1955), and works well for both fixed-wing aircraft and helicopters. It assumes that all the air passing through the *wing disk* (defined below) is deflected downwards through the same angle by the action of the wings. That is, a fixed downward *induced velocity* is assumed to be imparted to all the air passing through the wing disk, while the air round about is not affected.
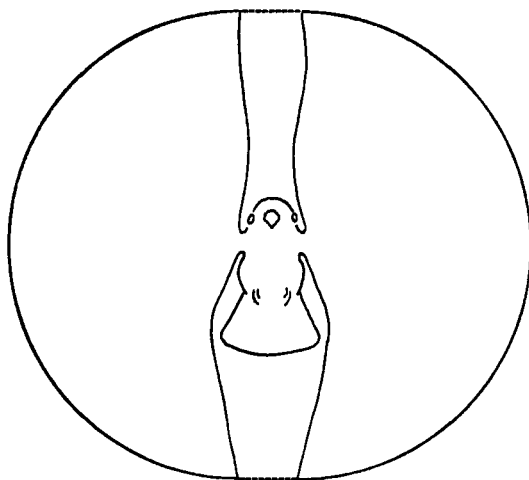

FIGURE 1. Disk area is defined as the maximum area which could be swept out by the wing tips—that is, the area inside the outer line, including that occupied by the body. It is slightly over-estimated by the approximate formula of equation (1).

The wing disk (Fig. 1) consists of two semicircles about the shoulder joints, joined together across the body, but it is sufficiently accurate to assume that the *disk area* S_d is

$$S_d = \tfrac{1}{4}\pi b^2, \tag{1}$$

where b is the wing span, that is the distance from wing tip to wing tip, measured with the wings fully spread.

The rate at which air passes through the wing disk, reckoned as mass of air flowing per unit time, is called the *mass flow*, and can be increased either by increasing the forward speed or by increasing the disk area. The greater the mass flow, the less induced velocity is needed to balance the weight, and the result is that the induced power is inversely proportional to the mass flow. At medium and high speeds the induced power P_i is

$$P_i = \frac{W^2}{2\rho S_d V}, \tag{2}$$

where W is the weight, ρ the air density and V the forward speed. This relation assumes that the mass flow through the wing disk is proportional to the forward speed, which becomes a poor approximation at very low speeds. At zero speed (hovering) the mass

flow is entirely due to the induced velocity, and in this case the induced power P_{th} is

$$P_{th} = \frac{W^{3/2}}{\sqrt{(2\rho S_d)}} \tag{3}$$

—not infinity as would be predicted by equation (2)!

If W, ρ and S_d are known, P_{th} can be calculated from equation (3), and joined on to a curve calculated from equation (2), as shown in Fig. 2. The low-speed portion of the curve, where this approximation is made, is not of particular interest in regard to migration, and equation (2) can be assumed to hold in the more significant region extending upwards from V_{mp}.
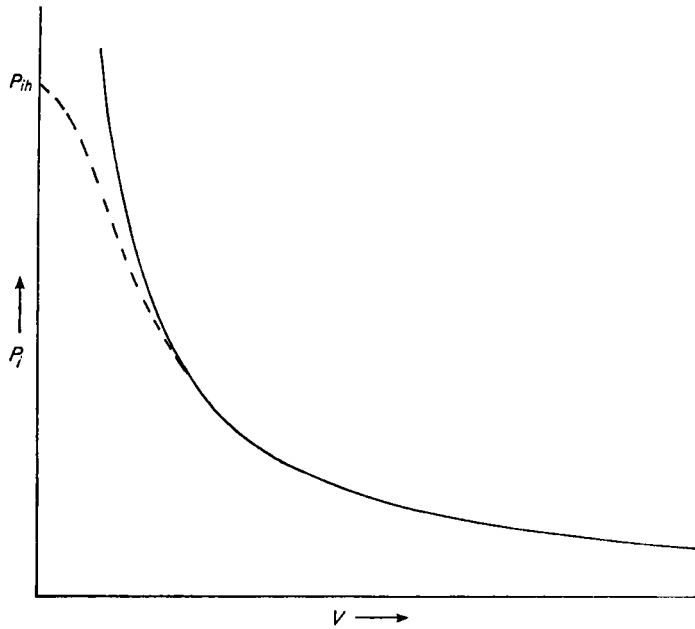

FIGURE 2. Approximate method of constructing curve of induced power versus speed. The solid line is a hyperbola calculated from equation (2). The point at zero speed, marked P_{th}, is calculated from equation (3), and may be joined to the hyperbola by eye. The dotted line shown is actually a calculated induced power curve for the pigeon (from Pennycuick 1968b).

(2) *Parasite power*

The bird's body experiences a backward drag force D_b, and if the bird is to travel along at a speed V in spite of this, a second component of power P_p is needed, where

$$P_p = D_b V. \tag{4}$$

P_p is called the *parasite power*, that is, the power needed to overcome the drag of non-lifting parts. The body drag D_b is itself a function of V, and is best understood in terms of an " equivalent flat-plate area " A. Such a plate is shown in Fig. 3 (a), immersed in a stream of air flowing past it at a speed V, and the plate is assumed to bring the air to a halt over the whole of its surface. In this case the drag force D experienced by the plate would be

$$D = \tfrac{1}{2}\rho A V^2. \tag{5}$$

Inert bodies of other shapes immersed in a stream of air generally also experience a drag force proportional to the square of the speed, provided the range of speeds considered is not too great. The drag of a reasonably streamlined object, such as a bird's body, is

less than that of a flat plate of equal frontal area. For example Pennycuick (1968a) found that the wingless body of a pigeon had a frontal area of 36 cm², but that its drag corresponded to that of a flat plate of 15·5 cm² area (Fig. 3 (b)). The pigeon's body is thus regarded as equivalent to a flat plate of area 0·43 times the body's frontal area.
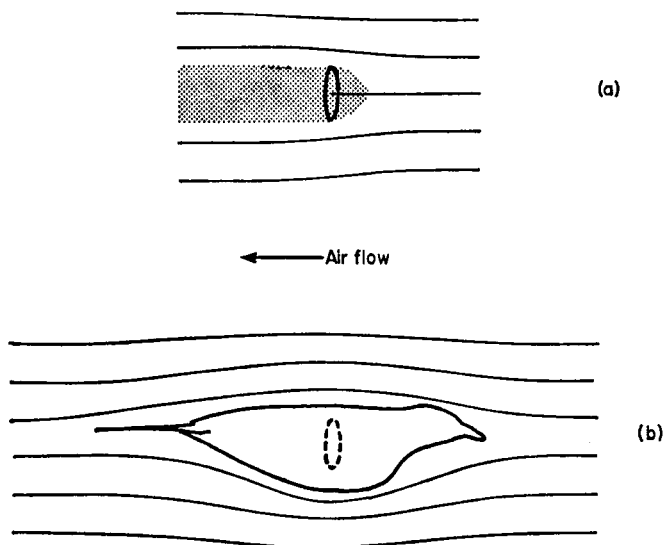

(a)

◄———Air flow

(b)

FIGURE 3. (a) The hypothetical flat plate stops the air completely over the whole of its area—the stippled zone represents stationary air.
(b) The drag of a streamlined object is equivalent to that of a flat plate of smaller frontal area (dotted outline).

It is not difficult to measure the drag of frozen birds' bodies mounted in a wind tunnel, and the equivalent flat-plate area is then easily determined from equation (5). A practical precaution which should be mentioned here is that it is extremely important to mount the specimen on a streamlined support—if a cylindrical support is used, drag measurements up to twice the real values can be obtained.

In the absence of actual measurements, the above figures for the pigeon can be scaled to give some idea of the equivalent flat-plate area of the body in other species. For geometrically similar birds, areas vary as the two-thirds power of the weight, so that if W is the weight of the bird in grammes, and A the equivalent flat-plate area of its body in square centimetres, then the relation

$$A = 15·5 \left(\frac{W}{400}\right)^{2/3} \tag{6}$$

will give a rough estimate of A. It will be seen later that V_{mp} and V_{mr} are not very sensitive to errors in A, so that a useful first approximation can be obtained from equation (6). Where better estimates are required, however, drag measurements should be made on frozen bodies.

From equations (4) and (5) the parasite power P_p required to overcome the drag of the body is

$$P_p = \tfrac{1}{2}\rho A V^3. \tag{7}$$

(3) *Profile power*

The third major component of power in flight is that required to overcome the profile drag of the wings. This component, the *profile power*, is the most difficult to

estimate, and consideration of its effects is deferred to p. 531. To start with, a curve of power versus speed will be derived by adding together induced and parasite powers only, and then the modifications resulting from adding profile power as well will be deduced.

PERFORMANCE CURVE FOR AN IDEAL BIRD

Neglecting profile power for the moment, a preliminary curve of power required versus speed can be constructed by adding together the induced power from equation (2) and the parasite power from equation (7). The total power P is then

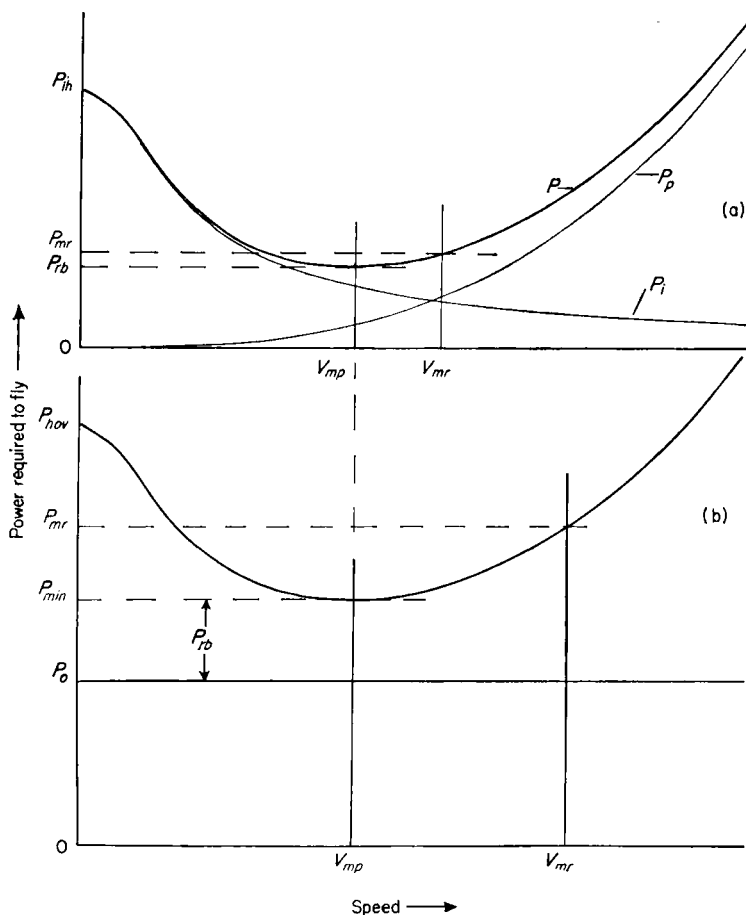$$P = \frac{W^2}{2\rho S_d V} + \tfrac{1}{2}\rho A V^3. \tag{8}$$

FIGURE 4. (a) Power versus speed curve for the ideal bird. The upper (thick) curve, marked P, is the total power required to fly. It is the sum of the induced power P_i and the parasite power P_p (thin curves). The power required to fly is a minimum at the speed marked V_{mp}, but maximum range is achieved at the higher speed V_{mr}. The corresponding powers are P_{rb} and P_{mr}.

(b) Power versus speed curve for real bird. The curve is the same shape as in (a), but a constant profile power P_0 has been added. The curves of P_i and P_p are omitted, being the same as in (a). V_{mp} is unchanged, but the minimum power required to fly is now $P_0 + P_{rb}$ and is marked P_{min}. V_{mr} is now higher than before—the ratio of V_{mr} to V_{mp} can be found from Fig. 5 if a value is assigned to the ratio of P_0 to P_{rb}. V_{mr} could be found by drawing a tangent to the curve from the origin, but an easier way, which does not involve plotting out the curve, is given in the text, and summarized in the Appendix.

This represents the performance curve of an ideal bird, that is, one whose wings generate lift without any profile drag. The minimum power speed V_{mp} can now be found by differentiating equation (8) and setting the first derivative equal to zero:

$$\frac{dP}{dV} = -\frac{W^2}{2\rho S_d V^2} + \frac{3}{2}\rho A V^2 = 0$$

whence

$$V_{mp} = \frac{0 \cdot 760 \, W^{1/2}}{\rho^{1/2} A^{1/4} S_d^{1/4}} . \tag{9}$$

V_{mp} can now be marked in on Fig. 4 (a). The power required at this speed (P_{rb}) is obtained by substituting V_{mp} from equation (9) in equation (8):

$$P_{rb} = 0 \cdot 877 \frac{W^{3/2} A^{1/4}}{\rho^{1/2} S_d^{3/4}} . \tag{10}$$

This may be thought of as the " rock-bottom power ", that is the lowest power with which the bird could conceivably remain airborne, if its wings were perfectly efficient.

For maximum range, the distance travelled per unit work done (which will later be translated into kilometres flown per gramme of fat oxidized) must be maximized. This ratio will be referred to as the specific range E, and at any particular speed V it is given by

$$E = \frac{V}{P}, \tag{11}$$

P being the power required to fly at that speed. The problem is to find the speed V_{mr} at which E is a maximum—in practice it is easier to find the speed for which its reciprocal $1/E$ is a minimum. From equation (8):

$$\frac{1}{E} = \frac{P}{V} = \frac{W^2}{2\rho S_d V^2} + \frac{1}{2}\rho A V^2. \tag{12}$$

Differentiating, and putting the first derivative equal to zero:

$$\frac{d}{dV}\left(\frac{1}{E}\right) = -\frac{W^2}{\rho S_d V^3} + \rho A V = 0$$

whence

$$V_{mr} = \frac{W^{1/2}}{\rho^{1/2} A^{1/4} S_d^{1/4}} . \tag{13}$$

Comparing this with equation (9), it is seen that V_{mr} is 1·32 times V_{mp} and can be marked in accordingly on Fig. 4 (a).

The power P_{mr} required to fly at V_{mr} for maximum range is then found by substituting for V_{mr} from equation (13) in equation (8):

$$P_{mr} = \frac{W^{3/2} A^{1/4}}{\rho^{1/2} S_d^{3/4}} . \tag{14}$$

Comparing with equation (10), P_{mr} is seen to be 1·14 times P_{rb}, and it too can now be marked on Fig. 4 (a).

EFFECTIVE LIFT: DRAG RATIO

Closely related to the specific range E is the effective lift: drag ratio $(L/D)_{eff}$, which is defined as

$$\left(\frac{L}{D}\right)_{eff} = \frac{WV}{P} \tag{15}$$

P being the power required to fly at speed V. $(L/D)_{eff}$ is a dimensionless ratio, and may be thought of as the ratio of the weight to the average horizontal force needed to propel the bird along. It is, of course, zero in hovering, and like E reaches a maximum at V_{mr} declining again at higher speeds. The maximum value of $(L/D)_{eff}$ attainable by the ideal bird, which will be called $(L/D)_{ult}$, can be found by substituting V_{mr} (from equation (13)) and P_{mr} (from equation (14)) in equation (15), whence

$$\left(\frac{L}{D}\right)_{ult} = \sqrt{\frac{S_d}{A}}. \tag{16}$$

The ultimate lift : drag ratio is thus easily estimated from its square, the disk : body ratio S_d/A. It must be remembered that the ultimate value of $(L/D)_{eff}$ calculated from equation (16) is that which would be obtained if the bird were flapping ideal wings, devoid of profile drag, and a real bird would be doing well to achieve half this value in practice. To obtain realistic estimates of effective lift : drag ratio, and also of the other key quantities whose " ideal " values are given by equations (3), (9), (10), (13) and (14), the effects of wing profile drag must now be taken into account.

PERFORMANCE CURVE OF A REAL BIRD

Pennycuick (1968a) found that the pigeon's wings create rather a large amount of profile drag, and as the wings have to be flapped whether the bird is flying fast or slowly, a substantial amount of power is needed to overcome this at all speeds. The profile power estimated for the pigeon (Pennycuick 1968b) is fairly constant in the region of V_{mp}, decreasing somewhat at very low speeds, and increasing somewhat at very high speeds. This immediately suggests an approximate method, used here, of allowing for profile power in rough performance estimates: a constant profile power P_0 is added at all speeds, thus converting the curve of Fig. 4 (a) into that of Fig. 4 (b). This approximation will probably lead to noticeable errors at very low speeds, but should be adequate in the medium speed region which is of the most interest in connection with migration.

PROFILE POWER RATIO

The magnitude of P_0 is difficult to estimate, and no easy method is yet available, but for analytical purposes it is most conveniently expressed in relation to P_{rb} (defined as in equation (10)). Calculations on the pigeon indicate that a value of P_0 equal to twice P_{rb} should be about right. This is expressed as a profile power ratio X, where

$$X = P_0/P_{rb}. \tag{17}$$

For the moment X will be taken as 2 for all flying animals, for want of better information. It is to be hoped that future research will provide methods of estimating X in different birds, and in this case the method explained below will allow the effects of profile power ratios between 0 and 3·5 to be assessed.

It cannot be too strongly emphasised that there is no theoretical reason why profile power should be exactly constant regardless of speed, or, even if it is, why X should be exactly 2. It is just that experimental and theoretical work to date suggests that the first assumption should be sufficiently close to the truth to give useful performance estimates, and the second, being the only estimate of X available at present, is as good a starting point as any.

EFFECT OF X ON PERFORMANCE ESTIMATES

It can be seen by comparing Fig. 4 (a) and 4 (b) that the addition of P_0 does not alter the minimum power speed, and so V_{mp} can be calculated from equation (9) as before. The power required P_{min} to fly at this speed is now, however,

$$P_{min} = P_{rb} + P_0 = P_{rb}(1 + X) \tag{18}$$

where P_{rb} is obtained from equation (10). P_{min} is an estimate of the true minimum power required to fly, with all major power losses allowed for.

Since the power is now increased by P_0 at all speeds, the lift : drag ratio is decreased (equation (15)), but more at speeds near V_{mp} than at speeds where the power required was already high. The speed V_{mr} for best lift : drag ratio (and hence maximum specific range) is thus higher in Fig. 4 (b) than in Fig. 4 (a). For any particular value of X, V_{mr} is always a fixed multiple of V_{mp}, and this relation is plotted in Fig. 5. For instance if X is 2, V_{mr} would be 1·72 V_{mp}.

P_{mr} is also increased, and here again it is a fixed multiple of P_{min} for any particular value of X. This relation is plotted in Fig. 6.

The maximum value of $(L/D)_{eff}$ is achieved at V_{mr} and will be called $(L/D)_{max}$. It is, of course, less than $(L/D)_{ult}$ as calculated from equation (16). For any assumed value of X, the ratio of $(L/D)_{max}$ to $(L/D)_{ult}$ can be read off the graph of Fig. 7.

By adding P_0 to the hovering induced power (equation (3)), the total power required to hover P_{hov} is
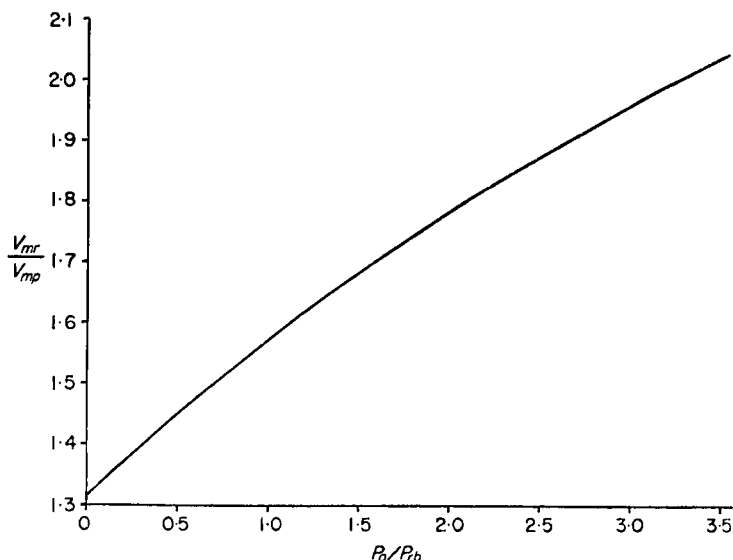
$$P_{hov} = P_0 + P_{th} = XP_{rb} + P_{th}. \tag{19}$$

FIGURE 5.   Ratio of V_{mr} to V_{mp} for different values of X, where $X = P_0/P_{rb}$ (see Fig. 4 (b)).
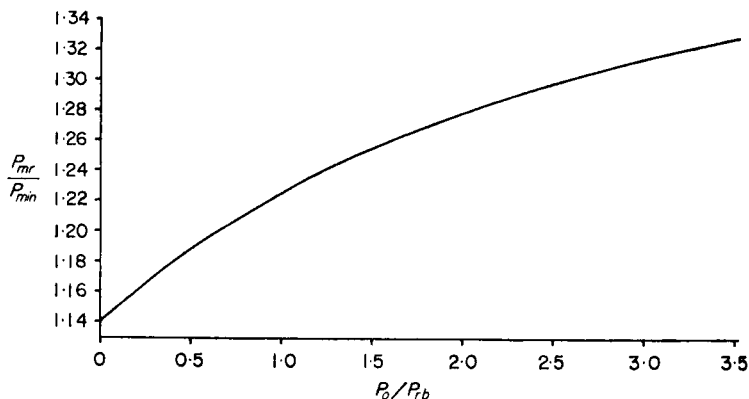

FIGURE 6.   Ratio of P_{mr} to P_{min} for different values of X (see Fig. 4 (b)).
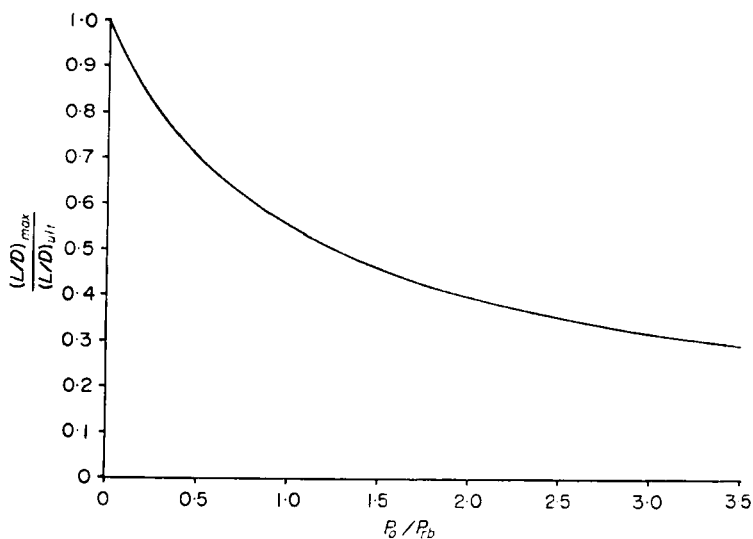
FIGURE 7.   Ratio of $(L/D)_{max}$ to $(L/D)_{ult}$ for different values of X.

SPEED RANGE

The two basic speeds V_{mp} (from equation (9)) and V_{mr} (from equation (13) and Fig. 5) may be said to define the lower and upper limits respectively of a bird's *speed range*. Many flying animals can, of course, fly slower than V_{mp} (even down to zero speed), and faster than V_{mr}, but there is not usually much point in doing either on migration (see p. 540 however). V_{mr} is the optimum speed to fly on migration, as it results in maximum range, and it can be assumed that birds which have enough muscle power to fly at V_{mr} will do so. Calculations of V_{mp} and V_{mr} are of great interest even if only approximate, since they give an idea of the speeds at which one may expect to find various flying animals travelling about—in general one will expect to find them migrating at speeds nearer V_{mr} than V_{mp}.

Figure 8 shows calculated speed ranges for a selection of flying animals plotted against body-weight. The line represents the proportionality 30 (p. 542), and shows that larger animals fly faster on the whole than smaller ones; the possible spread of speed ranges at any one body-weight is quite limited. Animals whose speed ranges lie to the right of the line are fast for their size, and those to the left are slow. On this basis it can be seen that there is not much to choose between the Lammergeier *Gypaetus barbatus*, the Pipistrelle *Vespertilio pipistrellus* and the Cabbage White *Pieris brassicae* which are all in the " main stream ", while the House Fly *Musca domestica* is rather a fast little creature for its size. The Common Tern *Sterna hirundo*, Montagu's Harrier *Circus pygargus*, Red Kite *Milvus milvus* and Frigate Bird *Fregata aquila* stand out as adapted for slow flight, and so also does the Wandering Albatross *Diomedea exulans*—its V_{mr} is about 20 m/sec, or 45 miles/h, but this is slow for a bird of this size. The Little Auk *Alle alle*, Willow Ptarmigan *Lagopus lagopus*, Razorbill *Alca torda* and Ruby-throated Hummingbird *Archilochus colubris* are noticeably faster than most, but there are no exceptionally fast birds heavier than about 1 kg. Only in the medium-sized insects, Bumble Bee *Bombus terrestris*, Honey Bee *Apis mellifera* and Blowfly *Calliphora vomitoria*, is there enough power to spare to get far to the right of the line—that is to cruise at an exceptionally high speed by using very short wings relative to the body-size and weight. The reasons for these limitations will emerge later.
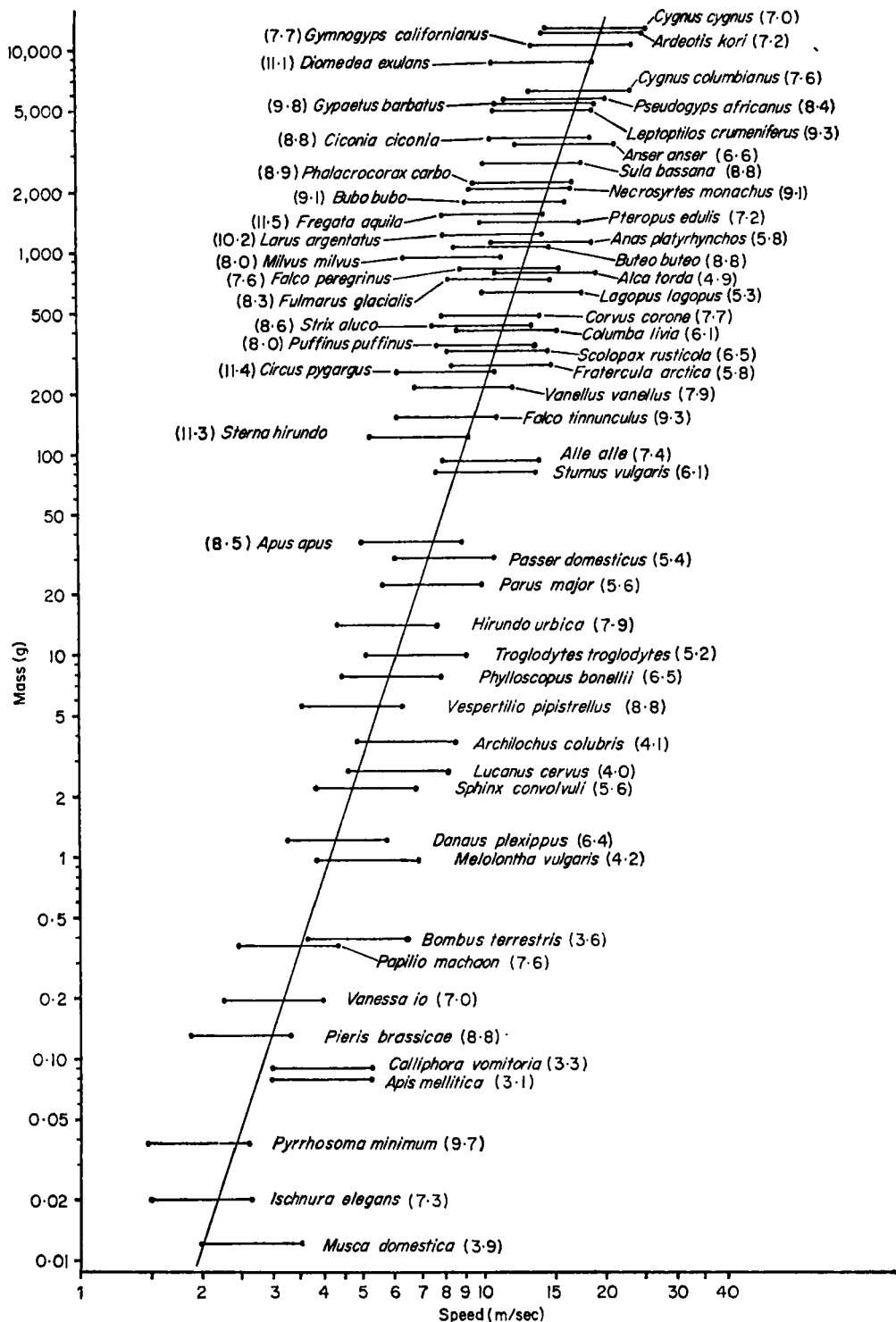
FIGURE 8. Calculated speed ranges for various flying animals. The left-hand end of each line represents V_{mp}, and the right-hand end V_{mr}—the latter, being the most economical cruising speed, is the more likely to be used on migration. Major approximations made in calculating speeds are: (1) equivalent flat-plate area of body is calculated from equation (6), (2) profile power ratio is taken to be 2 throughout, (3) weights are taken as recorded, and in most cases it is not known how much food or fat is included.

Numbers in brackets are estimates of $(L/D)_{max}$, assuming $X=2$. The line represents the proportionality $V \propto W^{1/6}$.

Sources of information: Greenewalt (1962); Wildfowl Trust (see Acknowledgments); author's own measurements.

Some of the calculated speed ranges are at variance with popular belief, but probably correct nonetheless. The Peregrine *Falco peregrinus* goes no faster than its prey the Pigeon *Columba livia*, and therefore is obliged to climb high and stoop on the passing pigeon, in order to get enough speed to overtake it. The flying fox *Pteropus edulis* goes almost as fast as the Mallard *Anas platyrhynchos*, while the Swift *Apus apus* is a slower bird than the House Sparrow *Passer domesticus*, the Great Tit *Parus major* or the Wren *Troglodytes troglodytes*, and only a little faster than the Stag Beetle *Lucanus cervus*. It may be that Swifts fly faster than V_{mr} during aerial displays, and that Flying Foxes fly nearer to V_{mp} owing to lack of power. The Swift's reputation for great speed could be due to its habit of diving past the observer at a higher speed than it can maintain in horizontal powered flight.

It can be objected that these calculated speed ranges are only approximate, and this is true. The calculation of V_{mp} is, however, straightforward, and based on well-established theory. The only data required are the weight, disk area, and equivalent flat-plate area of the body. The first two of these quantities are easy to measure, and only the third involves a substantial amount of guesswork, arising from the use of equation (6) in place of experimental measurements of A. However, equation (9) shows that V_{mp} varies with the fourth root of A, and is therefore not strongly affected by errors in A—if, for instance, the estimate of A were out by a factor of 2, the resulting estimate of V_{mp} would be out by a factor of less than 1·2.

Although the data used here are fragmentary and could be much improved, it would seem that this method of estimating speed ranges has less scope for error than the measurement of flight speeds by such methods as driving along beside a bird in a vehicle. It is almost impossible to allow accurately for wind with this method, and relative motion of bird and vehicle is difficult to allow for or eliminate. Similarly, timing a bird past two points with a stopwatch suffers from parallax errors, wind errors, and often uncertainty about the vertical motion of the bird or air as well. It also has to be remembered that in even a shallow dive a bird may considerably exceed the upper end of the " speed range " as defined here for horizontal flight, but measurements of high speeds attained by diving are of no relevance in computing migratory performance. For instance, pigeons may at times be seen flying at any speed between zero and at least 3 V_{mp}, but only a small part of this speed range, in the region of 1·8 V_{mp}, gives useful migratory performance. Spot measurements on free-flying pigeons, even if accurate, would give little idea of their cruising speed or range. Measurements of average speed over a long distance, such as those of Michener & Walcott (1967) are, of course, a different matter, but observations of this quality are difficult to obtain.

In general, spot measurements of flight speeds are of interest in themselves if demonstrably accurate, but are of limited use in the study of migration. It can be (and is) suggested that this is one instance where calculation is definitely to be preferred to any but the most laborious and difficult methods of measurement.

The numbers in brackets in Fig. 8 are estimates of $(L/D)_{max}$ calculated from equation (16) and the graph of Fig. 7. These estimates are more liable to error than the speed estimates, since, as Fig. 7 shows, effective lift : drag ratio (unlike V_{mp}) is strongly affected by profile power ratio. The latter has been assumed to be 2 throughout, for want of definite information on birds other than the pigeon, but may in fact vary widely in different birds and insects. However, the general indication that large birds tend to have better effective lift : drag ratios than small ones is probably a correct inference from body proportions, and one would expect this effect to be intensified by the fact that it is easier to achieve low profile drag at high than at low Reynolds numbers (Schmitz 1960).

Comparison of equation (16) with equation (9) also shows that $(L/D)_{eff}$ is more strongly affected by errors in estimating A than is V_{mp}.

MIGRATION RANGE

SIGNIFICANCE OF EFFECTIVE LIFT : DRAG RATIO

The effective lift and drag may be visualized as shown in Fig. 9. T is the average propulsive thrust which the bird has to exert, and this balances D, the average drag. L, the lift, balances the weight. Thus, if the weight is increased, L must also be increased, and if the effective lift : drag ratio remains the same, D (and therefore also T) will increase in proportion. Thus

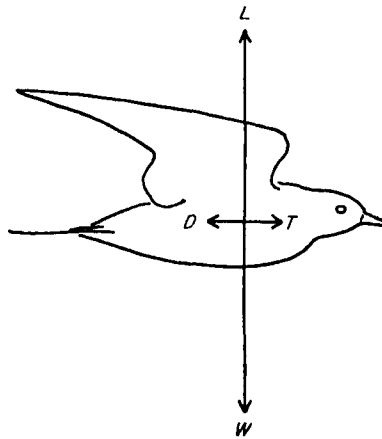$$T = W\left(\frac{D}{L}\right)_{eff} .$$

(20)

FIGURE 9. Forces on a bird in horizontal flight at a steady speed are in equilibrium, when averaged over a whole number of wing-beat cycles. They may be analysed into a lift force L balancing the weight W, and a thrust force T balancing the drag D. The effective lift : drag ratio L/D is also the ratio of weight to thrust.

The work done in flying one kilometre is equal to T times one kilometre, and by equation (20) is proportional to W. The amount of fuel used is therefore also proportional to W. In other words, any bird with a particular value of $(L/D)_{eff}$ consumes a fixed proportion of its weight in flying one kilometre, regardless of whether it is a large or a small bird.

Putting this another way, if a fixed proportion of the weight consists of fuel, the distance which can be flown on migration depends *only* on the lift : drag ratio. The number of air miles flown by, say, a swan and a hummingbird would be the same if both start with, say, 30% of their take-off weight as fuel, and if both have the same effective lift : drag ratio.

Various considerations modify this argument in practice:

(1) On the whole, small birds achieve somewhat lower effective lift : drag ratios that large ones (p. 535).

(2) Very large birds are limited in the extra weight they can carry, and are unable to devote such a large fraction of their weight to fuel as are smaller birds (p. 546).

(3) Small birds fly slower than large ones, and because of this are more affected by wind (pp. 533–539).

Combining equations (11) and (15), the specific range may be expressed in an alternative way as

$$E = \frac{1}{W}\left(\frac{L}{D}\right)_{eff} .$$

(21)

If c.g.s. units were used in equation (21), the weight would have to be expressed in dynes, and the specific range would come out in centimetres per erg. If the round-number approximations are made that 1 gf=10^3 dynes, and that oxidation of 1 g of fat yields 8,000 joules of mechanical work, then equation (21) can be more conveniently expressed as

$$E = \frac{800}{W} \left(\frac{L}{D}\right)_{eff} \tag{21a}$$

where W is now in grammes-force and E is in kilometres flown per gramme of fat consumed. For instance a 400-g pigeon with $(L/D)_{max}$ about six would be able to fly about 12 km/g of fat, while a 3·7-g Ruby-throated Hummingbird, with $(L/D)_{max}$ only 4·1, would cover nearly 900 km/g of fat.

It is important to note that equation (21a) refers to the *rate* at which fuel is used per kilometre flown at any particular instant in a flight, and during a long flight this changes progressively as fuel is used up and the weight diminishes. Equation (50) on p. 550, which takes account of this, should be used if it is required to calculate the actual distance flown on a given initial fuel load.
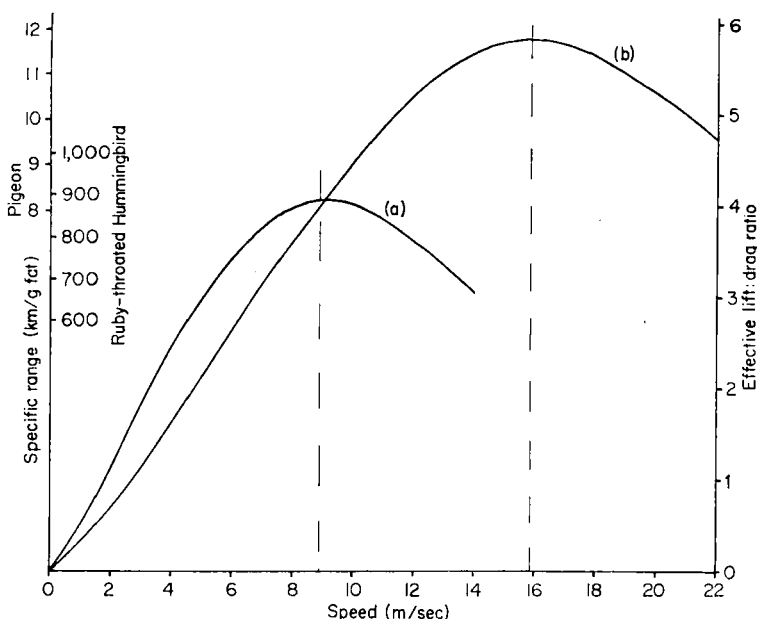

FIGURE 10. Calculated curves of effective lift: drag ratio (scale at right) versus speed for (a) the Ruby-throated Hummingbird, and (b) the Pigeon (from Pennycuick 1968b). The scales at left show specific range in km/g of fat. The vertical broken lines represent V_{mr}, the most economical cruising speed, for each bird.

Figure 10 shows calculated values of $(L/D)_{eff}$ plotted against speed for the pigeon and the Ruby-throated Hummingbird, with the corresponding specific range also shown. It can be seen that to obtain maximum range, a bird has only a limited choice of speeds at which it can fly. Fairly small deviations either faster or slower than V_{mr} result in noticeable loss of range. Figure 10 shows that the smaller bird must fly slower than the larger one, which is generally true. Some practical implications of this are considered on pp. 550–1.

MUSCLE EFFICIENCY

The maximum-range speed V_{mr} is here calculated on purely aerodynamical grounds: the calculation of range assumes that the flight muscles convert approximately 20% of the chemical energy consumed into mechanical work, regardless of speed or power output. In practice, the efficiency of the flight muscles (ratio of mechanical work done to chemical energy consumed) will be greatest at some particular power output, and will decrease at higher or lower powers, so diminishing the range achieved. It may, therefore, be to a migrating bird's advantage to vary its speed somewhat from V_{mr}, in order to match the power required to the optimum power output of the flight muscles. This complication cannot be allowed for without much more information on the mechanical properties of various birds' flight muscles, but the effect on cruising speed is not likely to be very large, as vertebrate locomotor muscles are generally tolerant of fairly wide deviations from maximum power without serious loss of efficiency (Hill 1950). Efficiencies somewhat higher than that assumed here, perhaps up to 25%, may possibly be achieved under optimum conditions, and if so, this would be reflected in increased range.

EFFECT OF WIND

The " wind ", as visualized by aviators, represents a large body of air moving along at some definite speed V_w in a particular direction. The bird or aeroplane is embedded in this moving air, and flies at a speed V_a *relative to the air*: V_a is called its *airspeed*, and all speeds considered so far are airspeeds. The bird's *groundspeed*, that is, the speed and direction with which it travels over the ground, is the vector sum of its airspeed and the windspeed.

The specific range E of equation (11), which is based on airspeed, refers to the *still-air* range, and the alternative version of equation (21a) gives *air* kilometres flown per gramme of fat consumed. The object of migration is to cover kilometres over the ground rather than through the air, and in practical performance estimates the effect of wind must be taken into account, and range calculated in terms of groundspeed rather than airspeed. To consider first the two simplest special cases, if the wind happens to blow in the same direction as the bird is heading (tailwind) the bird's groundspeed is $V_a + V_w$, whereas if the wind direction is opposite to the bird's heading (headwind) its groundspeed is $V_a - V_w$. The actual specific range E_g achieved over the ground is then, from equation (11),

$$E_g = \frac{V_a - V_w}{P} \tag{22}$$

for a headwind, and

$$E_g = \frac{V_a + V_w}{P} \tag{23}$$

for a tailwind, as against the still-air specific range E_a, which is

$$E_a = \frac{V_a}{P}. \tag{24}$$

The ratio of the achieved range to the still-air range is thus

$$\frac{E_g}{E_a} = 1 - \frac{V_w}{V_a} \tag{25}$$

for a headwind, and

$$\frac{E_g}{E_a} = 1 + \frac{V_w}{V_a} \tag{26}$$

for a tailwind.

These ratios are plotted against airspeed, for various windspeeds, in Fig. 11, and estimated values of V_{mr} for various animals are marked. It can be seen that a wind of a given speed has much less effect on the range of a fast animal than on that of a slow one. For instance, a light headwind of 5 m/sec (9·7 knots) would suffice to drive a Cabbage White cruising at 3·5 m/sec, rapidly backwards, while a Trumpeter Swan *Cygnus c. buccinator*, cruising at 26 m/sec, would achieve over 80% of its still-air range against a wind of this strength. A pigeon could achieve nearly 70% of its still-air range against such a wind, a Swallow *Hirundo rustica* less than 40%. A headwind of 10 m/sec would reduce even the larger migrants to less than 50% of their still-air range, while Swifts, kites and small passerines would make no significant progress. Tailwinds, of course, have the opposite effect, and this is shown on the scale at the right-hand side of Fig. 11.
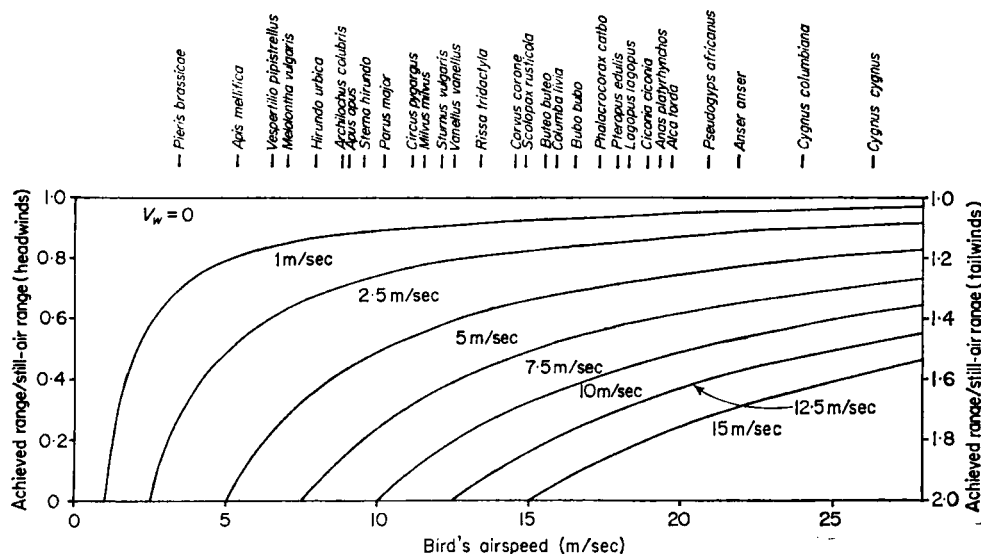

FIGURE 11. Effect of head- and tailwinds on specific range for eight windspeeds, from 0 to 15 m/sec. The effect on the specific range for a bird flying at a given airspeed is read off the scale at left for a headwind, or off that at right for a tailwind. Calculated cruising speeds (V_{mr}) for various animals are marked.

Winds which are not parallel to the bird's heading change its direction as well as its speed: the extent to which a bird's track over the ground is deflected by a wind of any speed and direction has been calculated by Evans (1966), together with the results of various methods of compensation open to the bird. It will suffice here to consider another special case, a crosswind blowing at right angles to the bird's heading, which produces an increase of speed, and also a change of direction θ, where

$$\theta = \tan^{-1}\left(\frac{V_w}{V_a}\right). \qquad (27)$$

Crosswinds of moderate strength thus deflect slow birds through a large angle, but have less effect on faster ones.

In general the slower (and hence smaller) the animal, the more it is affected by wind. The groundspeed of tiny insects like aphids (Aphididae) is almost entirely due to the wind, to such an extent that oriented migration is unprofitable, and they rely entirely on dispersal by the wind. Land-birds which make a sea or desert crossing on their regular migrations must carry a sufficient fuel reserve to cope with any headwind which is at all likely to spring up while they are airborne—and a headwind of 5 m/sec must surely be a normal

hazard to migrants in most parts of the world. If this is so, then Fig. 11 shows that the smaller migrants would have to carry a fuel reserve of the order of 100% of the still-air requirement to give a reasonable margin of safety, and the larger ones 50%. This need to carry excessive fuel reserves rather erodes the competitiveness of small birds in regard to migration range.

When flying against a headwind it is advantageous to fly somewhat faster than V_{mr} if possible: a bird flying at V_{mr} achieves its maximum still-air range, but if there is a headwind of V_{mr} it gets nowhere relative to the ground. By flying a little faster, it will lose some still-air range (Fig. 10) but will at least make some progress over the ground. Loss of range due to flying against a headwind cannot be prevented, but it can be reduced somewhat by flying faster than V_{mr}, if sufficient power is available to do this. Small animals are better placed than large ones in this respect, on account of their better power margin (see below).

ENDURANCE

The argument of p. 536 indicates that all birds whose lift : drag ratios are equal should achieve the same still-air range on a full load of fuel. Since small birds go slower than large ones, this means that small birds can remain continuously airborne for longer than large ones. In fact, the time spent in the air on a given load of fuel should vary inversely with the square root of the weight

$$t \propto \frac{1}{\sqrt{W}}. \qquad (28)$$

Although the endurance is not usually of significance in itself on migration, it may become important in emergencies, especially if a migrant is blown far off course and becomes lost over the sea. The best course then may be to slow down to V_{mp} and remain airborne for as long as possible in the hope of being carried to land by the wind, and in this situation a small animal, having longer endurance, has a better chance of survival than a large one. The American passerines and Monarch butterflies *Danaus plexippus*, which occasionally arrive in Britain after prolonged westerly gales, have probably made use of this tactic.

GENERAL PERFORMANCE LIMITATIONS

The merits of flying at different speeds and power levels have so far been discussed on the general assumption that flying a animal can produce enough power to fly in whatever way best suits the purpose in hand. In fact the difficulty of meeting power requirements varies from one animal to another, and in general is greater in large than in small animals. At very large sizes the difficulty becomes so acute as to set a definite upper limit to the size and weight of practicable flying birds, and migration range begins to be curtailed at a size and weight well below this ultimate limit.

MAXIMUM POWER AND THE PERFORMANCE CURVE

The performance which a bird can attain depends on the relation between the power versus speed curve of Fig. 4 (*b*) and the maximum power available from the flight muscles. In practice two " maximum powers " must be distinguished:

(1) Absolute maximum power P_{max}, attainable in a brief burst of maximal exertion.

(2) Maximum continuous power P_{mc}, the greatest power which can be kept up steadily for a long period.

In general P_{max} is likely to be limited by the mechanical limitations of the flight muscles, and P_{mc} by the maximum rate at which the bird can absorb oxygen.

Figure 12 shows a hypothetical power versus speed curve with horizontal lines representing P_{mc} marked in at three different levels. Line (a) would represent a bird which
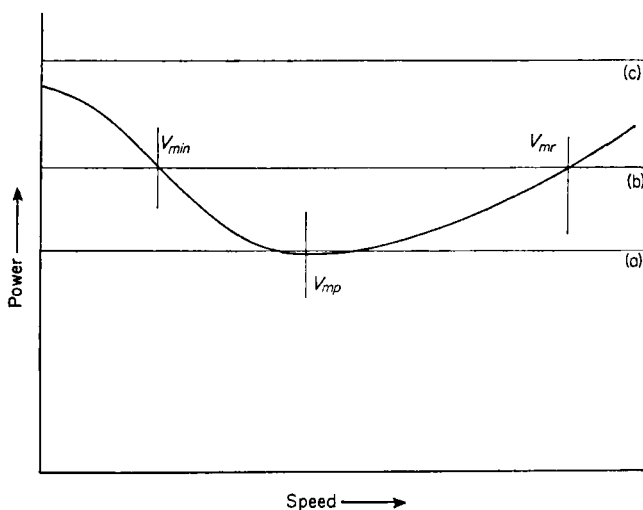
FIGURE 12. Relation of power available (horizontal lines) to power required (curve). Line (a) represents a bird with just enough power to fly, but only at one speed, V_{mp}. Line (b) represents one with enough power to fly at any speed between V_{mr} and V_{min}. Line (c) represents one with enough power to hover.
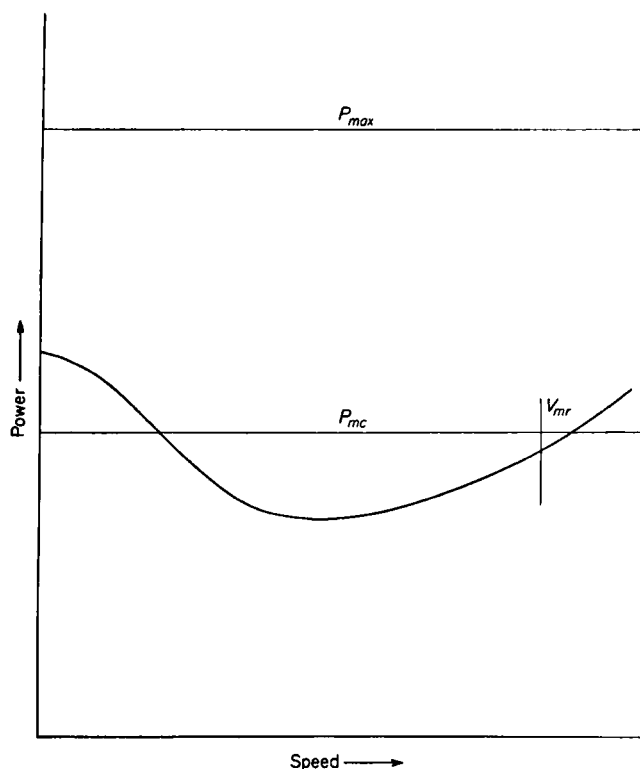

FIGURE 13. Calculations on the pigeon (Pennycuick 1968b) indicate that its maximum continuous power (P_{mc}) somewhat exceeds that needed to fly at V_{mr}, while its absolute maximum (sprint) power P_{max} is nearly twice as great. The ratio of P_{max} to P_{mc} probably varies widely in different birds.

had just sufficient power to fly, but could only go at V_{mp}—it would be unable to maintain height either faster or slower than this. Line (b) is a more practical bird with sufficient power to cruise at V_{mr}, thus achieving its maximum range. If it so wished, it would also be able to cruise at lower speeds, down to the speed marked V_{min} in the diagram. Line (c) represents a bird which, like a hummingbird, can hover without incurring an oxygen debt.

Figure 13 shows the situation thought to prevail in the pigeon (Pennycuick 1968b), where P_{mc} is high enough to permit cruising at V_{mr}—or perhaps a little faster—whereas P_{max} is nearly twice as great, sufficient to allow the pigeon not only to hover briefly, but also to climb vertically for a few feet.

EFFECT OF INCREASING SIZE

It was shown by Pennycuick (1968b), from a general dimensional argument, that one would anticipate a sharp upper limit to the mass of practicable flying animals, and it was conjectured on empirical grounds that the limit for birds is in the region of 12 kg (measured with the crop empty). This argument, which depends on comparing the power required to fly with that available from the flight muscles, will now be developed in greater detail in order to show how increasing size progressively restricts a bird's capabilities, and also to allow the known capabilities of certain very large species to be related to actual mechanical conditions in their flight muscles.

If one compares geometrically similar birds of different sizes, the weight W, disk area S_d and equivalent flat-plate area of the body A will all be greater in a large bird than in a small one. Both S_d and A, being areas, should vary with the two-thirds power of the weight:

$$\left. \begin{array}{c} S_d \propto W^{2/3}, \\ A \propto W^{2/3}. \end{array} \right\} \quad (29)$$

Substituting the proportionalities (29) in equation (13), the way in which the speed for maximum range should depend on the weight in different-sized birds can be deduced:

$$V_{mr} \propto \frac{W^{1/2}}{(W^{2/3})^{1/4}(W^{2/3})^{1/4}} = W^{1/6}. \quad (30)$$

Thus, to achieve maximum range, large birds must fly faster than small ones. By equation (20) the thrust the bird has to exert is proportional to the weight. The power required is equal to the thrust times the speed, so that

$$P_{mr} = TV_{mr} \propto W \times W^{1/6} = W^{7/6}. \quad (31)$$

Large birds thus require more power per unit weight than small ones to fly at their maximum-range speed (or at their minimum-power speed for that matter). If bird (A) weighs twice as much as bird (B), it would require not twice as much, but $2^{7/6}$, or 2·24 times as much power to fly.

One might expect that large birds would have relatively more flight muscle than small ones, but apparently this is not so. Greenewalt (1962), after collecting and analysing a large amount of published data, found that the combined weight of pectoralis and supracoracoideus muscles averages about 17% of the body weight in birds of any size, and there is no systematic change in this percentage correlated with body-weight.

POWER AVAILABLE FROM THE FLIGHT MUSCLES

The difficulties of large birds are further aggravated by the fact that less power is available from each gramme of muscle in a large bird than in a small one. The reason for this is easily understood if the power output is considered in terms of the tensile stress, specific shortening and contraction frequency prevailing in the muscle.

Considering the hypothetical muscle shown in Fig. 14, it has an extended length l, and when it contracts, it shortens a distance Δl. The *specific shortening* λ is defined as

$$\lambda = \frac{\Delta l}{l}. \tag{32}$$

Similarly the stress S is the force exerted per unit cross-sectional area. If the total force is F and the cross-sectional area is a, then
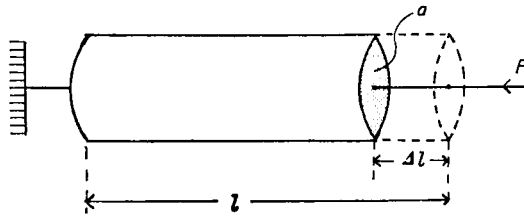
$$S = \frac{F}{a}. \tag{33}$$

FIGURE 14. A hypothetical muscle, anchored at the left-hand end, shortens through a distance Δl, from its extended length l. It exerts a force F while doing so, and its cross-sectional area (stippled) is a.

The work done ΔQ in one contraction is
$$\Delta Q = F \Delta l. \tag{34}$$
Now if λ and S were constant, then it would follow from equations (32) and (33) that
$$\Delta l \propto l$$
and
$$F \propto a. \tag{35}$$
Combining the proportionalities (35) with equation (34),
$$\Delta Q \propto la = H$$
$$\propto W \tag{36}$$
where H is the volume of the muscle, which in turn is proportional to its weight. Thus in muscles of different size and shape, whose specific shortening and attainable stress are the same, the work done in one contraction should be proportional to the weight, and to the mass—that is, the *specific work*, or work $\bar{Q}$ done per gramme of muscle in each contraction, should be constant.

$$\bar{Q} = \frac{\lambda S}{\rho m}, \tag{37}$$

ρm being the density of muscle. For instance, a vertebrate locomotor muscle, which might possibly achieve a stress of 2·5 kgf/cm² in maximal exertion, and with a specific shortening of perhaps 0·25, might produce a specific work of about 0·057 joule/g (taking ρm as 1·06 g/cm³).

The *specific power* $\bar{P}$, or power output per gramme of muscle, is the product of the specific work and the contraction frequency f:

$$\bar{P} = \bar{Q} f. \tag{38}$$

For reasons of structural integrity, which are explained by Hill (1950), large animals are obliged to oscillate their limbs at lower frequencies than small ones, and in general contraction frequency decreases with the one-third power of the body weight:

$$f \propto W^{-1/3}. \tag{39}$$

Since $\bar{Q}$ is independent of the body weight, equation (38) and proportionality (39) imply that

$$\hat{P} \propto W^{-1/3}. \qquad (40)$$

That is, the power available from each gramme of flight muscle is inversely proportional to the one-third power of the body-weight, so that the total power available P_a varies with the two-thirds power of the weight:

$$P_a \propto W^{2/3}. \qquad (41)$$

POWER MARGIN

In the very largest flying birds, such as the Kori Bustard *Ardeotis kori*, the power available from the flight muscles is marginally sufficient to fly. An example of this species shot by the author weighed 11·9 kg wt, and had a wing span of 247 cm. Its estimated minimum power at 5,000 feet (1,520 m) (ground elevation in typical habitat) would be 350 w, and the total mass of its flight muscles was 1,950 g. The minimum specific power required would thus be 0·18 w/g. An observation of flapping frequency* gave 3·1 /sec at take-off, yielding a figure of 0·058 joule/g for the specific work of the flight muscles. Thus the estimate made on p. 543, that 0·057 joule/g is about the maximum specific work which could reasonably be expected from vertebrate locomotor muscle, indicates that this bird would be barely able to stay airborne, and that only at one speed (15·5 m/sec). Flapping flight at the maximum-range speed (estimated as 27·6 m/sec), requiring 450 w, would hardly be feasible.

The behaviour of the Kori Bustard is quite consistent with this assessment. It is a mainly cursorial species which takes to the air only if hotly pursued, and requires a long, fast take-off run to get off the ground. Once airborne, it flies low over the ground for a short distance, and lands as soon as it is out of reach of its pursuers. It seems that the Kori Bustard is like the hypothetical bird of Fig. 12 (a)—it must use all its flight muscle at maximum power to fly at all, and can only go at one speed.

In a pigeon, on the other hand, of mass 400 g and with 90 g of flight muscle, the power required to maintain the maximum-range speed (16 m/sec) works out at 10·3 w, calling for a specific power (continuous) of 0·11 w/g. The flapping frequency at this speed is 5·5/sec, so that the specific work required is only 0·020 joule/g. From equation (37) it can be seen that the pigeon, flying at its maximum-range speed, must be running its flight muscles either (a) at a lower stress, or (b) at a lower specific shortening, or (c) both, than the Kori Bustard flying at its minimum-power speed.

It is probable that λ is in fact less since the wing-beat amplitude at V_{mr} in the pigeon is only about 0·64 of the maximum possible, so one could interpret this to mean that the specific shortening of the flight muscles is about 0·13, instead of 0·20 as assumed for the Kori Bustard. The stress in this case would still be relatively modest, however, about 1·6 kgf/cm². One would expect the flight muscles to be able to carry more stress than this, and can conclude that either (a) the fibres are being run below their maximal stress or (b) only part of the flight muscle is active in cruising flight. The latter is undoubtedly the case in the pigeon, whose pectoralis muscle consists of about four fifths red muscle adapted for continuous running, and one fifth white fibres suitable only for bursts of anaerobic activity (George & Berger 1966).

The contrast between these two birds clearly shows the difficulties resulting from large size, expressed in the proportionalities (31) and (41). The Kori Bustard needs to use the whole of its flight muscles at maximum power in order to fly at the minimum-power speed, and it is most unlikely that it could ever achieve its maximum-range speed, even in a brief sprint. The pigeon, however, when cruising at its maximum-range speed,

* I am indebted to Mr. R. Brock of the B.B.C. for enabling me to make this measurement from a film taken by him.

can not only fly with a reduced wing-beat amplitude, but can still afford to use only four-fifths of its flight muscle, reserving the other fifth for take-off and other strenuous manoeuvres.

Smaller birds have a still greater margin of power available over that required for cruising flight. This seems to be reflected in the generally poorer values of $(L/D)_{max}$ which their body measurements indicate (Fig. 8)—evidently small birds can tolerate low lift : drag ratios, and no doubt gain in manoeuvrability and other forms of flexibility as a result. In addition, small migratory species make use of their favourable power margin to carry much larger fuel loads (relative to fat-free weight) than larger birds could lift. This question of maximum fuel load will be considered next.

OPERATIONAL LIMITATIONS

EFFECT OF CARRYING EXTRA WEIGHT

When a bird accumulates fat, or carries a heavy load of food in its crop or talons, the extra weight results in more power being required to fly, and also in maximum range being achieved at a higher speed. From equation (13),

$$V_{mr} \propto \sqrt{W} \tag{42}$$

and from equation (14)

$$P_{mr} \propto W^{3/2}. \tag{43}$$

The argument here is somewhat different from that above, since now only the weight is changing, with no corresponding change in S_d and A. Actually A will be affected by taking on fuel, but this effect will be neglected to start with, and taken up below (p. 548).
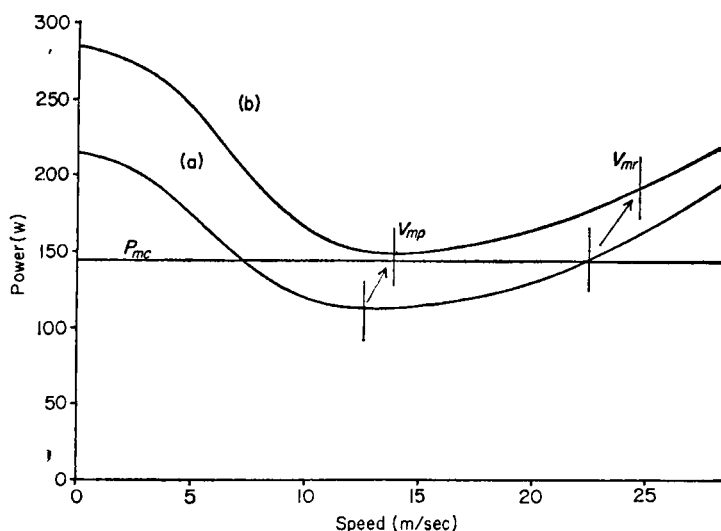

FIGURE 15. Calculated power curves for the White-backed Vulture, (a) with crop empty, and (b) carrying a load of 1,140 g. If P_{mc} is assumed to be just sufficient to fly at V_{mr} with the crop empty, the vulture should have been unable to fly when loaded (it was, see text).

In the case of a bird like the Kori Bustard, which is barely able to fly even without any additional load, any extra weight at all would prevent it from becoming airborne. This species in fact has a very small crop, and appears to subsist on a continual trickle of small vegetable matter, without building up big fuel stores. The larger African vultures A egypiinae), of mass 5–7 kg with the crop empty, are unable to exist in this way because

of the intermittent and unpredictable nature of their food supply. They compete with formidable mammalian scavengers, especially hyaenas and lions, and when they happen on a corpse, they have no alternative but to eat as much and as fast as possible. The ability to carry extra weight is therefore important for these birds.

One White-backed Vulture *Pseudogyps africanus* which the author shot weighed 5·5 kgf after emptying the crop. Its performance curve was estimated as in Fig. 15 (a). Another one was caught, heavily gorged on the remains of a dead zebra, and was induced to disgorge its crop contents, which amounted to 1,140 gf. This increase in weight would result in the revised power curve of Fig. 15 (b). Now, White-backed Vultures probably can fly at V_{mr} when the crop is empty, as they can often be seen in the early morning flying horizontally for a mile or two over the Serengeti Plains, for instance. The horizontal line in Fig. 15 (a) is drawn on this assumption, and it can be seen that even if the bird has as much power available as this, a crop load of 1,140 g would prevent it from flying at all. In fact, the gorged bird could not fly, and was picked up by hand after a brief chase in a vehicle. After disgorging its crop contents it leapt into the air without a take-off run (but against a wind of 2–3 m/sec) and flew off.

UPPER LIMITS OF WEIGHT

These observations on the Kori Bustard and the White-backed Vulture provide round-number estimates for two limiting weights—12 kgf as the limit for birds able to fly horizontally at all, and 6 kgf as the limit for flying horizontally at V_{mr}, carrying no extra load.

The upper limit of around 12 kgf, to which living birds seem to be subject, could possibly be exceeded by specialization of the wings for cruising or soaring flight, but this would involve some sacrifice of take-off performance, which is also a factor in determining the maximum size of ecologically practicable birds (Pennycuick 1968b). In some circumstances, take-off requirements may be relaxed somewhat, as in mountain birds which can normally launch from a cliff or down a slope, or in birds inhabiting windy seas, which can launch into wind from the crest of a wave. There may have been special situations in the past in which flying birds larger than any alive today could survive, and certain fossil flying birds appear to have been somewhat larger than the largest living birds. For instance, the giant Miocene sea-bird *Osteodontornis orri* is thought to have had a wing span of at least 430 cm (Howard 1957), while the mass of the Pleistocene Cathartid vulture *Teratornis merriami* (Miller 1925) has been estimated by Howard (1955) at around 20 kg. Howard attributes the abundance of these huge vultures in the La Brea tar deposits in California to their becoming entangled in the tar whilst devouring the remains of mammals already trapped, and this danger would no doubt have been greatly aggravated by marginal take-off performance, and the need for a long take-off run. Speculation about the way of life of the even larger teratorn *T. incredibilis* (Howard 1952), known only from a single gigantic cuneiform bone, should perhaps be deferred until more of its skeleton comes to light.

It may be noted that man-powered aircraft are not subject to the same upper weight limit as flying animals, because the propeller or flapping wing can be geared to work at a lower frequency than the pilot's muscles—thus escaping from the limitation set by proportionalities (39) and (40).

SMALLER BIRDS

Turning now to smaller flying animals, a number of widely different species have been recorded carrying loads as great, or nearly as great as their fat-free weight. Odum, Connell & Stoddard (1961) found that Scarlet Tanagers *Piranga olivacea* can store fat before migration up to 52% of the body-weight, and some other passerines can take on nearly as much: R. B. Ransome (pers. comm.) found in a study of the Greater Horseshoe

Bat *Rhinolophus ferrum-equinum* that the average weight of adults is around 15 gf, but that pregnant females near term can weigh up to 30 gf: Rothschild & Clay (1952) state that a female gnat *Culex pipiens* weighing 1·4 mgf can take on 1·2 mgf of blood. One can infer from this that even where muscle power available is not the limiting factor, it is difficult—presumably for structural reasons—to construct a flying system versatile enough to cope with a weight range of more than 2 : 1.

If the body-weight is doubled, V_{mr} is increased, and equation (14) shows that the power required to achieve maximum range increases by a factor of $(2)^{3/2}$, that is 2·83. Equations (31) and (41) imply that for birds of different size the ratio of power available P_a to power required P_r varies inversely with the square root of the (fat-free) body-weight:

$$\frac{P_a}{P_r} \propto \frac{1}{\sqrt{W}}. \tag{44}$$

Now if this ratio is one in the Kori Bustard, which at 12 kg is thus regarded as the heaviest bird able to fly, then from equation (44), the heaviest bird able to achieve 2·83 times the minimum power required to fly would have a mass of 1·5 kg. This, of course, refers to absolute maximum power available, and minimum-power speed. By analogy with the White-backed Vulture the upper limit for birds able to double their weight and still achieve maximum range would then be 750 g. Figure 16 represents an estimate of the total load which a bird should be able to carry, expressed as a function of body-weight.
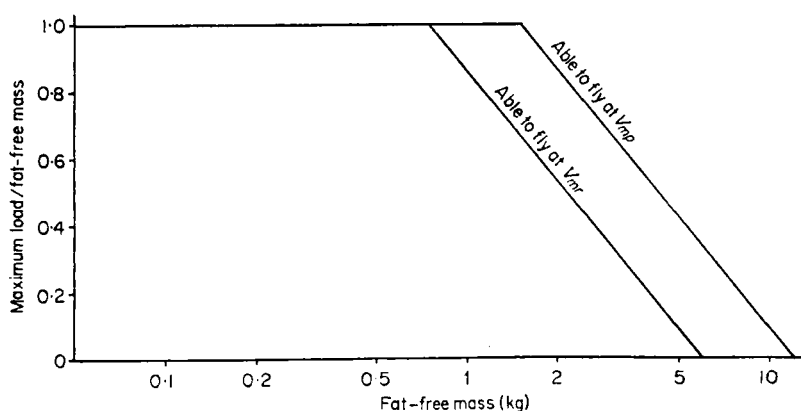

FIGURE 16. Small or medium-sized birds can carry a load (food or fat) equal to their fat-free mass, and still fly at V_{mr}. Above about 6 kg (fat-free), any additional load restricts the speed to below V_{mr}: above about 12 kg any extra load prevents horizontal flight altogether.

TECHNIQUES OF MIGRATION

These relationships are clearly reflected in the different methods of migration used by different birds. Small and medium-sized birds, perhaps up to 700 or 800 g fat-free, are all on an equal footing in that they can carry a load of fuel of the same order as their own fat-free mass. This means that all would have the same range if their lift : drag ratios were equal, but on account of the trend shown in Fig. 8, whereby smaller birds tend to achieve lower effective lift: drag ratios, the best long-range non-stop migrants are to be found among the larger birds of this category, such as the larger waders. Also the largest members of the group able to carry a full fuel load are on the whole the fastest, and therefore least affected by adverse winds (Fig. 11).

On exceeding 700 or 800 g (fat-free), it remains possible to fly at doubled body-weight, but not at the maximum-range speed. Maximum lift : drag ratio cannot be obtained until some fuel has been used up, and the distance flown per gramme of fat consumed during

the early part of the flight is reduced accordingly. There will probably still be some gain from taking on a full fuel load, even if the flight has to start at less than the optimum speed, but the range achieved will be less than that of birds which can fly at V_{mr} with a full load.

Birds above 1·5 kg fat-free should not be able to fly at all with a fuel load equal to the fat-free weight, and the maximum load they can carry decreases progressively, down to zero at about 12 kg or a little above. The effect of this is clearly seen in the techniques used by large migrants such as the various eagles (Accipitrinae—2 kg) and storks (Ciconiidae—3–4 kg) which migrate between northern Europe and Africa. These birds cover most of the distance by thermal soaring, a means of travel which, while slower than straight flapping flight, consumes hardly any fuel. In this way their limited fuel reserves can be made to suffice for very long migratory flights.

Geese and swans (Anserini) are of especial interest, as they include large species which are apparently able to migrate without soaring. It would be extremely interesting to investigate the maximum fuel loads which these birds can carry, and the greatest distances which they can fly non-stop, especially in the largest migratory species (*Cygnus c. cygnus* and *C. c. buccinator*), which are among the heaviest of flying birds. The explanation of their capabilities probably lies partly in high aerodynamic efficiency—their bodies look better streamlined than those of most birds, and their tapered, pointed wings may well consume less profile power than the square-ended, slotted wings typical of large thermal-soaring birds. On the other hand, the belief that migrating swans and geese do not soar might be worth re-examining, as it is quite possible that some of them might regularly use lee wave systems to conserve energy on their regular migrations. It would be interesting to analyse the migration routes of the larger species, to see if there is any tendency for them to lie parallel to, and downwind of, ranges of hills, and transverse to prevailing winds.

A numerical example of migration range in a Swan is considered on p. 550.

EFFECT OF FUEL LOAD ON EFFECTIVE LIFT : DRAG RATIO

Equation (16) shows that if the body dimensions remain constant, extra weight should have no effect on the lift : drag ratio. In this case the bird loaded with fuel would use more power, but would also go faster, so that the distance covered per gramme of fuel oxidized would remain the same. In practice, however, the fuel load must be put
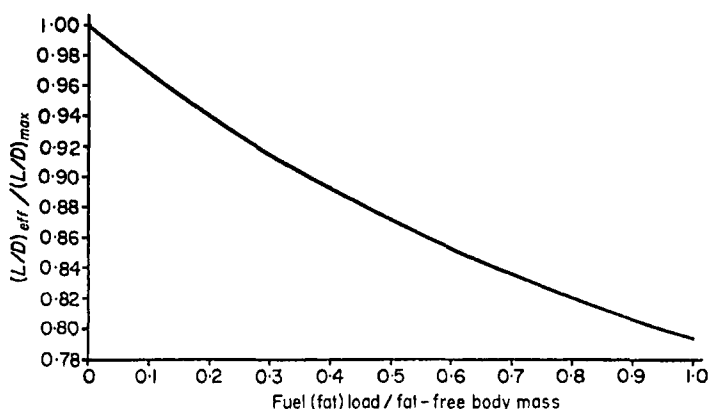

FIGURE 17. Decrease in effective lift : drag ratio due to storing fat. This is due to the increased bulk, and hence drag, of the body, not to the increase in weight as such. The latter would have no effect on $(L/D)_{eff}$ if body dimensions remained the same.

somewhere, and the body of a bird with a large fat store will normally be distended, so increasing A. One would expect that, approximately,

$$A \propto W^{2/3}. \tag{45}$$

In this case, if

$$\left(\frac{L}{D}\right)_{eff} \propto \sqrt{\frac{S_d}{A}} \tag{16a}$$

it follows that

$$\left(\frac{L}{D}\right)_{eff} \propto W^{-1/3}. \tag{46}$$

A bird carrying a fuel load equal to its fat-free weight should then be able to achieve an effective lift : drag ratio 0·79 times the maximum attainable when unloaded. The decline of effective lift : drag ratio with extra weight is plotted on the basis of equation (46) in Fig. 17. This is probably nearer the truth than assuming that $(L/D)_{eff}$ is unaffected by fuel load.

CRUISING TECHNIQUE AND RANGE ON A LONG FLIGHT

CHANGES OF SPEED AND POWER DURING CRUISE

A bird which sets out on a migratory flight carrying a fuel load equal to its fat-free weight, and keeps going until its fuel is all used up, would have to reduce speed (and therefore power) progressively during the flight in order to keep flying near its (progressively decreasing) maximum-range speed. The changes required are large—the speed at the beginning of the flight would be 1·4 times that at the end (equation (13)), and the power at the beginning would be 2·8 times that at the end (equation (14)). The range flown per gramme of fat consumed is proportional to the lift : drag ratio (progressively increasing, Fig. 17) and inversely proportional to the weight (progressively decreasing), the combined result being that a gramme of fat consumed at the end of the flight would suffice to cover 2·5 times as much distance as one consumed soon after take-off.

RANGE ON A LONG FLIGHT

The effect of changing lift : drag ratio is not very great, and an adequate approximation to the range obtained on a long flight can be made by neglecting this, and considering only the effect of the diminishing weight. Taking the usable energy content per gramme of fat to be K, then from equation (21), the *rate* at which mass is converted into distance (Y) flown is

$$\frac{dY}{dM} = - \frac{K}{Mg} \left(\frac{L}{D}\right)_{eff} \tag{47}$$

where M is the mass of the bird at any particular instant, and g is the acceleration due to gravity. This assumes that all the mass change is due to oxidation of fat, i.e. that no water, other than the metabolic water, is lost as well. If the bird sets off with an initial mass M_1, which dwindles to M_2 by the end of the flight, then, integrating equation (47), the total distance flown is

$$Y = - \frac{K}{g} \left(\frac{L}{D}\right)_{eff} \int_{M_1}^{M_2} \frac{dM}{M}$$

$$= \frac{K}{g} \left(\frac{L}{D}\right)_{eff} \cdot \log_e \left(\frac{M_1}{M_2}\right). \tag{48}$$

This can be less cumbersomely expressed in terms of a " range factor " R, where

$$R = \log_e \left(\frac{M_1}{M_2} \right) \qquad (49)$$

and R may, of course, equally well be expressed in terms of the starting and finishing weights W_1 and W_2:

$$R = \log_e \left(\frac{W_1}{W_2} \right). \qquad (49a)$$

PRACTICAL RANGE CALCULATIONS

If K is taken to be 8×10^{10} ergs per gramme, and g to be 981 cm/sec², then equation (48) may be expressed in the practical form

$$Y = 820\ R \left(\frac{L}{D} \right)_{eff} \qquad (50)$$

where Y, the air distance flown, is now expressed in kilometres. The appropriate value of R can be read off the graph of Fig. 18, against the percentage of the take-off weight consisting of fat. $(L/D)_{eff}$ is estimated from equation (16) and Fig. 7, as before. Reference to Fig. 11 allows the effect of headwinds of various strengths on the range to be estimated assuming that the bird (which would probably be ignorant of the wind strength unless
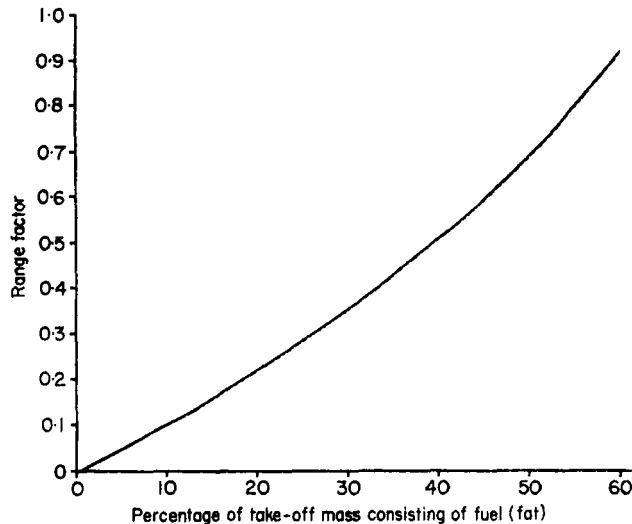

FIGURE 18. Range factor expressed as a function of the percentage of the take-off mass consisting of fuel. For use in calculating still-air range from equation (50).

close to, and in sight of solid ground) flies at V_{mr} regardless of wind strength. Three hypothetical examples may be given:

(1) A Whooper Swan, with $(L/D)_{eff} = 7.0$, starts with one-tenth of its weight as fat, so from Fig. 18, $R = 0.104$. Total air distance flown $= 820 \times 0.104 \times 7.0 = 600$ km.

Flying against a headwind of 5 m/sec the Swan would achieve 80% of its still-air range (from Fig. 11), i.e. 480 km. Against a wind of 10 m/sec it would go 360 km.

If the range is known from migration records, the argument can be inverted to give an estimate of a bird's actual lift : drag ratio, and hence of its profile power ratio. Suppose, for instance, that it were shown that 10% of the weight is indeed the maximum which a Whooper Swan can devote to fat, and still fly at V_{mr}. Suppose, further, that these birds

are known to fly non-stop from the Outer Hebrides to Iceland (720 km), with sufficient fuel reserve to give them an air range of, say, 900 km. The effective lift : drag ratio needed to achieve this would be

$$\left(\frac{L}{D}\right)_{eff} = \frac{900}{820 \times 0.104} = 11.4.$$

With $(L/D)_{ult} = 17.3$ (from equation (16)), Fig. 7 shows that the profile power ratio would have to be 0·63. This is very much better than the pigeon, but is quite conceivable.

(2) A pigeon starts with one fifth of its weight as fat, so from Fig. 18, $R = 0.223$. With $(L/D)_{eff} = 6.0$, the still-air range would be $820 \times 0.223 \times 6.0 = 1,100$ km. Figure 11 shows that this would be cut to 750 km against a wind of 5 m/sec, and to 400 km against a wind of 10 m/sec.

(3) A Ruby-throated Hummingbird starts with half its weight as fat, so from Fig. 18, $R = 0.693$. With $(L/D)_{max} = 4.1$, still-air range is $820 \times 0.693 \times 4.1 = 2,300$ km. A head-wind of 5 m/sec would reduce this to 1,000 km, whereas one of 10 m/sec would drive the creature backwards!

It may be noted that the actual weight of the bird is not required for the calculation of still-air range, for the reasons explained above. The weight is, of course, needed to find V_{mr}, which must be done before the effect of wind can be assessed.

EFFECT OF ALTITUDE

As altitude is increased, both the density and temperature of the air decrease. Although the density at any particular altitude changes somewhat from place to place and time to time, the values selected for the I.C.A.O. Standard Atmosphere (Table 1) give a close enough guide for most practical purposes. Equations (13) and (14) show that as

TABLE 1. *Air density in the I.C.A.O. standard atmosphere.*

HEIGHT ABOVE MEAN SEA LEVEL (FEET)	AIR DENSITY G/CM³
0	1.22×10^{-3}
1,000	1.19×10^{-3}
2,000	1.15×10^{-3}
3,000	1.12×10^{-3}
4,000	1.09×10^{-3}
5,000	1.06×10^{-3}
6,000	1.02×10^{-3}
7,000	9.94×10^{-4}
8,000	9.64×10^{-4}
9,000	9.34×10^{-4}
10,000	9.04×10^{-4}
11,000	8.76×10^{-4}
12,000	8.49×10^{-4}
13,000	8.22×10^{-4}
14,000	7.96×10^{-4}
15,000	7.70×10^{-4}
16,000	7.45×10^{-4}
17,000	7.21×10^{-4}
18,000	6.98×10^{-4}
19,000	6.76×10^{-4}
20,000	6.53×10^{-4}
21,000	6.31×10^{-4}
22,000	6.09×10^{-4}
23,000	5.90×10^{-4}
24,000	5.68×10^{-4}
25,000	5.49×10^{-4}

density decreases, the maximum-range speed increases, and so does the power required to fly at this speed:

$$V_{mr} \propto \frac{1}{\sqrt{\rho}},$$

$$P_{m_r} \propto \frac{1}{\sqrt{\rho}}. \tag{51}$$

Since both speed and power change in the same way with decreasing density, the effective lift : drag ratio is independent of air density (equation (15)). A bird flying high thus achieves the same range as one flying at sea level (equation (21)), but must cruise at a higher speed, with a corresponding increase in power output, and hence of its oxygen consumption. For instance, at 22,000 feet, where the density is about half its sea level value, the bird would have to increase both its cruising speed and its oxygen consumption to $\sqrt{2}$ times the sea level values.

OPTIMUM HEIGHT FOR MIGRATION

Although there is no gain in still-air range, it is advantageous to fly high because the increased cruising speed results in shorter flight time, and less interference from wind— although this latter advantage may be offset on particular occasions by stronger, or unfavourable winds aloft.

Another advantage of flying high results from the fact that the temperature drops, on verage, about 2°C per 1,000 feet of altitude, so that a bird can fly in much colder air with quite a modest increase of height. This can result in a substantial reduction of evaporative water loss, since the lower the ambient temperature, the more heat can be lost by convection, and the less water is required for cooling. For instance Tucker (1968) found that a budgerigar flying in a wind tunnel at 9·7 m/sec at an air temperature of 36–37°C dissipated about 47% of the waste heat generated in the flight muscles by evaporation, whereas at 18–20°C only 15% of the heat lost could be accounted for in this way. It would appear that most of the remaining heat is lost by convection from the thinly feathered ventral surface of the wing (Eliassen 1962).

In general, then, it is advantageous to fly as high as possible on migration, and the limit to the practicable cruising height would seem to be set by availability of oxygen. As the air density drops, so the maximum rate at which oxygen can be absorbed, and hence the maximum continuous power output (p. 540), also drops. However, by proportionality (51), the power required to fly at the maximum-range speed progressively increases, and there must be some height at which the maximum rate of oxygen absorption is just sufficient to maintain V_{mr}. This is the optimum height for migration, since if the bird climbs any higher than this it will be unable to maintain the maximum-range speed, and its lift : drag ratio and hence its range will suffer accordingly (Fig. 10). In piston-engined aircraft, which seem to be quite closely analogous to birds in this respect, the optimum cruising height is easily found by experiment—one simply climbs until the engine can no longer maintain the required speed, and then descends until it just can. Probably migrating birds use the same technique, as Eastwood & Rider (1965) found in a study with height-finding radar that individual migrants maintained remarkably constant heights, although birds, so far as is known, have no sense organ which would give a direct and accurate indication of altitude.

As fuel is used up during a long flight, the reduced weight results in less power being needed to maintain the maximum-range speed, so that the rate at which oxygen is required progressively decreases. The optimum height for migration therefore gradually increases, and one would expect migrant birds to climb gradually during the cruise phase of a long flight, in order to maintain the optimum height. This " cruise climb " technique is well known in aircraft practice.

INITIAL CLIMB AND FINAL DESCENT

During the climbing phase of a migratory flight, the bird must do work equal to the product of its weight and the height to which it climbs, in addition to the aerodynamic work already considered. This work is converted into potential energy, which is recoverable, since it can be used to glide down at the end of the flight, so converting height into distance without having to do any work on the glide. On a very long flight, the weight lifted to cruising height in the initial climb will appreciably exceed that remaining on the final glide, and in this case up to half the potential energy gained in the initial climb may be lost.

This does not result in any loss of range, however. If the bird climbs to a height h, thus acquiring potential energy Wh, it can be seen from equation (21) that the distance Y it could fly horizontally for the same amount of energy is

$$Y = h \left(\frac{L}{D} \right)_{eff}. \tag{52}$$

Thus if the bird climbs to a typical cruise height of, say, 2 km, and has a typical $(L/D)_{eff}$ of, say, 6, the work done in climbing would correspond to that needed to travel 12 km horizontally. At the end of the flight the bird can glide down at an angle of 1 in 6, thus covering the last 12 km without doing any work at all. This argument is not affected by changes of weight during the flight: it assumes only that the lift: drag ratio in gliding is the same as the effective lift: drag ratio in horizontal flight, which is approximately true in the pigeon.

CONCLUSION

The theory developed here leads to conclusions of two different types. In the first place there are general statements about the shape of the power curve, the effects of altitude and so forth, which are expressed in algebraic terms rather than in numbers: the reasoning leading to conclusions of this kind is derived from classical aeronautical theory, and although it may turn out to be oversimplified in places, it is unlikely to be fundamentally misleading. Secondly, formulae are provided for calculating numerical performance estimates for individual species of flying animals. The accuracy of these estimates depends not only on the correctness of the theory, but also on the accuracy of the experimental data required in the formulae. Direct experimental figures are available at present for only a very few kinds of flying animals, and these have to be extrapolated to cover other kinds by using dimensional arguments, which apply strictly only to geometrically similar animals flying at the same Reynolds Number. Such incautious extrapolation has been freely employed in the present paper, especially in preparing Fig. 8, and errors can result from this which are not due to any basic error in the theory. The difficulty can only be overcome by accumulating experimental measurements on different kinds of flying animals, and if this is done, it should eventually become possible to assign limits of error to performance estimates for a variety of flying animals.

SUMMARY

A theory is presented for calculating the relation between mechanical power required to fly and forward speed, for a bird flying horizontally. The significance of this for migration is explained, and quick methods are given (and summarized in the Appendix) for calculating key points on the curve.

Speed ranges and effective lift : drag ratios are calculated for a number of different flying animals.

Factors affecting migration range are discussed, and the effects of head- and tailwinds are considered. Still-air range depends on effective lift : drag ratio, but not on size or weight as such.

The relation of power required to that available from the muscles is considered. Small birds have a greater margin of power available over power required than large ones, and tend to run their flight muscles at a lower stress, or lower specific shortening, or both. There is an upper limit to the mass of practicable flying birds, represented approximately by the Kori Bustard *Ardeotis kori.*

The effect of adding extra weight (food or fuel) is to increase both minimum-power speed, and maximum-range speed, in proportion to the square root of the weight, and to increase the corresponding powers in proportion to the three-halves power of the weight.

Birds up to about 750 g (fat-free) can double their fat-free mass, and still have sufficient power to fly at the maximum-range speed. Larger birds are progressively more severely limited in the maximum loads they can carry, and this reduces their range. Many large birds migrate by thermal soaring, thus economizing on fuel at the expense of making slower progress.

During a long flight both speed and power have to be progressively reduced as fuel is used up. A formula is given for calculating the still-air range of a bird which does this in an optimal fashion. The only data required are the effective lift : drag ratio, and the proportion of the take-off mass devoted to fuel.

Increase of height has no effect on the still-air range, but the optimum cruising speed (and power) is increased. The optimum cruising height is reached when the bird can absorb oxygen just fast enough to maintain the required power. The optimum height increases progressively as fuel is used up.

No range is lost as a result of the work done in climbing to the cruising height.

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LIST OF SYMBOLS

A	Equivalent flat-plate area of body	P_{ih}	Induced power in hovering
a	Cross-sectional area of muscle	P_{min}	Power required to fly at V_{mp} (minimum power)
b	Wing span		
D	Drag	P_{mr}	Power required to fly at V_{mr}
D_b	Drag of the body	P_p	Parasite power
E	Specific range (distance flown/g of fat oxidized)	P_{rb}	" Rock bottom " power (minimum power for ideal bird)
E_g	Specific range achieved over the ground	P_o	Profile power
E_a	Specific range relative to the air	$\bar{P}$	Specific power (power/g of muscle)
F	Force exerted by muscle	$\triangle Q$	Work done in one contraction by muscle
f	Contraction frequency		
g	Acceleration due to gravity	$\bar{Q}$	Specific work (work done in one contraction/g of muscle)
H	Volume of muscle		
h	Cruising altitude	S	Tensile stress developed by muscle
K	Usable energy content per gram of fat (mechanical work)	S_d	Disk area
		T	Thrust
L	Lift	t	Endurance
$(L/D)_{eff}$	Effective lift : drag ratio	V	Forward speed
$(L/D)_{ult}$	Ultimate lift : drag ratio (ideal bird)	V_a	Bird's airspeed
$(L/D)_{max}$	Maximum achievable lift : drag ratio (real bird)	V_w	Windspeed
		V_{mp}	Minimum-power speed
l	Extended length of muscle	V_{mr}	Maximum-range speed
$\triangle l$	Distance shortened during contraction by muscle	W	Weight of bird
		W_1	Weight at take-off
M	Mass of bird	W_2	Weight after fuel exhausted
M_1	Mass of bird at take-off	X	Profile power ratio
M_2	Mass of bird after fuel exhausted	Y	Horizontal distance flown
P	Power	λ	Specific shortening of muscle
P_a	Power available from muscles	ρ	Air density
P_r	Power required to fly	ρ_m	Density of muscle
P_{hov}	Power required to hover	θ	Drift angle
P_i	Induced power		

APPENDIX

The following is a summary of the steps involved in quickly estimating a bird's performance. It is not necessary to calculate speeds and powers before estimating still-air range, but the maximum range speed must be estimated before the effects of headwinds on range can be allowed for.

BASIC DATA

(1) Measure weight.

(2) Measure wing span. Calculate disk area from equation (1).

(3) Determine equivalent flat-plate area of body, from wind tunnel measurements if possible. If no data available, estimate from equation (6).

(4) Decide profile power ratio. If no data available, try $X=2$ (equation (17)).

(5) Select air density appropriate to altitude from Table 1.

UNITS

Before using any more formulae, it is essential to ensure that all quantities required are expressed in mutually compatible units, such as those of the centimetre-gramme-second system, or the foot-pound-second system. The appropriate c.g.s. units are as follows:

(1) Weights should be expressed in dynes. To convert grammes weight to dynes, multiply by 981, or by 1,000 for rough calculations. Exceptions are certain practical formulae, which require weight to be in grammes-force, as mentioned in the text and also in this summary. 1 kgf=2·205 lbf.

(2) Areas should be in square centimetres. 1 inch=2·54 cm.

(3) Speeds will come out in centimetres per second.

(4) Powers will come out in ergs per second. 1 w=10^7 ergs per second. 1 kw=1·34 horsepower.

(5) Profile power ratio and lift : drag ratio, being dimensionless, have no units, and come out the same whatever system of units is used.

SPEEDS

(1) Find the minimum-power speed from equation (9).

(2) To find the maximum-range speed, multiply the minimum-power speed by the appropriate factor, read off Fig. 5.

POWERS

(1) Find the " rock bottom " power from equation (10).

(2) Find the true minimum power from equation (18).

(3) To find the power at the maximum range speed, multiply the minimum power by the appropriate factor, read off Fig. 6.

(4) Find the hovering power from equation (19).

The three key points on the power versus speed curve can now be marked, as in Fig. 4 (b).

OXYGEN AND FAT CONSUMPTION

The oxygen consumption in ml/min can be roughly estimated by multiplying the power in watts by 15, and adding a fixed allowance for basal metabolism. The latter can be estimated from data given by Lasiewski & Dawson (1967). To estimate the rate of consumption of fat in grammes/hr, multiply the power (in watts) by 0·45.

RANGE

(1) Find the ultimate lift:drag ratio from equation (16), and multiply by the appropriate factor from Fig. 7 to give an estimate of the true maximum effective lift:drag ratio.

(2) Find the specific range from equation (21a) if required, but do not use this to calculate the range achieved on a long flight. Express the weight in grammes-force for use in equation (21a).

(3) To find the air range on a long flight, decide what proportion of the take-off weight is to consist of fuel, and find the corresponding range factor from Fig. 18. Find range in kilometres from equation (50). The weight is not required in this formula.

(4) Assume that the bird flies at V_{mr}, and assess the effect of head winds on range from Fig. 11.

Dr. C. J. Pennycuick, Department of Zoology, University College Nairobi, P.O. Box 30197, *Nairobi, Kenya.*