BIRD METABOLISM DURING FLIGHT:
EVALUATION OF A THEORY

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INTRODUCTION

A theory that accurately predicts the energetic cost of avian flight from a small number of easily measured parameters could be useful, for measurements of metabolic rate during flight under controlled conditions are difficult to make. Pennycuick (1969) has recently presented such a theory. However, the power requirements predicted by this theory for level flight at different speeds have not yet been compared with measured values. In this paper, I will compare the predictions of Pennycuick's theory with the measured power requirements of budgerigar (Tucker, 1968) and the laughing gull (Tucker, 1972) in level flight at various speeds, and with some other data. Then I will add some new features to the theory and adjust its parameters so that the predictions fit the measured values more closely.

UNITS AND ACCURACY

The International System of Units, based on the metre (m), kilogram (kg) and second (s), is used throughout this paper. In this system, weight, measured in newtons, is distinguished from mass, measured in kg. The relation between the two is $W = mg$ where $g = 9.81$ m/s^2. The term 'power' describes energy transfer per unit time and is given in watts. One watt equals 0.860 kcal/h. Power input (P_i) is the rate at which free energy is released from substrates by oxidative metabolism, and the total power input is synonymous with one of the common definitions of metabolic rate. Power output (P_o) is the rate at which mechanical work is done by the system under consideration. For example, the power output of the flapping wings is the rate at which kinetic energy is added to the air. A speed of 1 m/s equals 3.60 km/h or 2.24 miles/h. The density of air in this study is 1.18 kg/m^3, which describes air at sea level at a temperature of 23 °C and a relative humidity of 70% (Hodgman, 1959).

Accuracy is defined in terms of systematic error and imprecision as recommended by Eisenhart (1968) and Ku (1969).

COMPARISON OF PENNYCUICK'S THEORY WITH MEASUREMENTS

Pennycuick estimates the power output during flight at a given speed as the sum of three terms: induced power, profile power and parasite power. (These terms will be explained in detail later.) Power input is then calculated as the power output

divided by the efficiency of the power-producing system, plus the basal metaboli rate. The theory can be represented by the following equations:

$$P_o = \frac{W^2}{2\rho S_d V} + \frac{A\rho V^3}{2} + \frac{1\cdot75 W^{\frac{3}{2}} A^{\frac{1}{4}}}{\rho^{\frac{1}{4}} S_d^{\frac{3}{4}}}, \tag{1}$$

where

$$S_d = 0\cdot785 b^2 \tag{2}$$

$$W = mg \tag{3}$$

and

$$A = 0\cdot00285 m^{\frac{2}{3}}. \tag{4}$$

Thus

$$P_i = P_o/E + P_{i,B} \tag{5}$$

where $E = 0\cdot2$ and

$$P_{i,B} = 3\cdot73 m^{0\cdot273}. \tag{6}$$

The symbols are described in Table 1, and the equations and numerical values have been assembled from Pennycuick (1969), either directly or after converting units to the International System. If wing span for equation (2) is unknown, it may be estimated from body mass by the relation

$$b = 1\cdot1 m^{\frac{1}{3}}. \tag{7}$$

This equation represents the curve fitted by Greenewalt (1962, his fig. 1) to data for a variety of birds excepting hummingbirds ranging in size from about 0·004 to 10 kg.

For comparison with equation (5) the measured power input of a budgerigar in level flight with a mass of 0·035 kg and a wing span of 0·235 m is

$$P_i = 0\cdot180\,(V-9\cdot7)^2 + 3\cdot52 \tag{8}$$

(Tucker (1972), calculated from his equation [26]). The comparable equation for a laughing gull with a mass of 0·322 kg and a wing span of 0·930 m is

$$P_i = 0\cdot090 V^2 - 1\cdot29 V + 23\cdot9 \tag{9}$$

(Tucker (1972), calculated from his equation [24]).

Pennycuick's theory also predicts how the power input of a bird flying at a given speed will vary as the mass of the bird changes. This prediction can be compared with measured values for a laughing gull flying at 10·8 m/s with different body masses at different times (Tucker, 1972). The prediction is made by allowing m to vary appropriately in equations (3) and (4) above, but not in equation (6) for basal metabolic rate. The basal metabolic rate will be little affected by mass changes since the added mass is presumed to be mostly fat. The measured values are given by

$$P_i = 36\cdot4 m^{0\cdot325}, \tag{10}$$

where the exponent has 95% confidence limits of 0·05 and 0·60 (Tucker, 1972).

Finally, the predictions of Pennycuick's theory can be compared with the 'cost of transport' (Tucker, 1970) measured for flying animals of various sizes. The cost of transport is a dimensionless number that expresses the minimum energetic cost to carry a unit of body weight over unit distance, and hence is given by $P_i/(WV)$ at the particular speed where this ratio has a minimum value. The cost of transport is functionally related to body weight in flying animals by the equation

$$P_i/(WV) = 0\cdot896 W^{-0\cdot227} \tag{11}$$

(calculated from Tucker, 1970).

Table 1

Symbols

A equivalent flat plate area
b wing span
c exponent for (Re) effect on profile power
C_D drag coefficient
C_L lift coefficient
D drag
E efficiency
F proportionality constant for profile power
g acceleration of gravity (9.81 m/s^2)
j energy equivalent of oxygen (20×10^6 joules/m^3)
K proportionality constant
l length
L lift
m mass
p pressure
P power
ρ density
Q cardiac output
R' correction factor for induced power
(Re)   Reynolds number
S area
S_d area of actuator disc
t time
U blood velocity
μ air viscosity
V flight velocity
V_0 velocity for determination of A (11.0 m/s)
V'_0 velocity for reference (Re) for profile power
$\dot{V}_{O_2}$ rate of oxygen consumption
W weight

Subscript symbols

a	arterial	par	parasite
B	basal	pu	pulmonary
h	heart	pr	profile
i	input	r	respiration
in	induced	s	systemic
o	output	v	venous

Pennycuick's theory fits the measured values for power input of the budgerigar and the gull at various speeds remarkably well, although it does not account for the rapid increase in the power input of the budgerigar at low speeds (Figs. 1, 2). At intermediate speeds the largest deviations from the theory are 10% for the budgerigar and 0% for the gull. The theory is less successful at predicting how the power input for flight of the gull changes with body mass (Fig. 3). Neither does it predict accurately the cost of transport for birds with weights much different from 3 N (0.3 kg) (Fig. 4). For the smallest (0.03 N, 0.003 kg) and largest (100 N, 10 kg) birds, the predicted costs of transport are low and high respectively by factors of more than 2. These discrepancies might be only partly due to failure of the theory, for the measurements are scattered and are from only a few, perhaps peculiar, species. At any rate, Pennycuick's theory is a useful method of estimating metabolic rate during flight of the budgerigar and the gull at intermediate speeds.

The theory can be modified to fit the empirical curve for cost of transport more closely without much sacrifice of the agreement shown in Figs. 1 and 2. Although
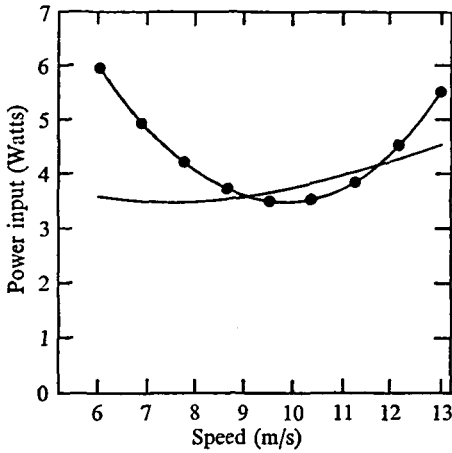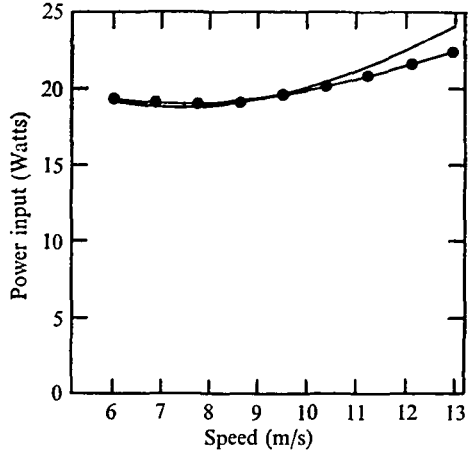
Fig. 1

Fig. 2

Fig. 1. The metabolic rates of a budgerigar flying at different speeds as predicted by measurements (beaded line, equation (8)) and by Pennycuick's theory (plain line). The budgerigar has a mass of 0·0350 kg, a wing span of 0·235 m and an equivalent flat plate area of 0·258 × 10⁻³ m².

Fig. 2. The metabolic rates of a laughing gull flying at different speeds as predicted by measurements (beaded line, equation (9)) and by Pennycuick's theory (plain line). The laughing gull has a mass of 0·322 kg, a wing span of 0·93 m and an equivalent flat plate area of 1·58 × 10⁻³ m².
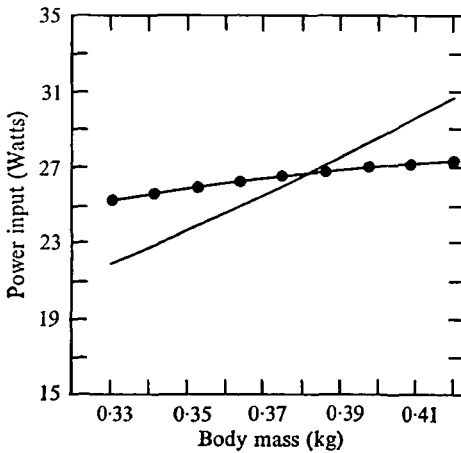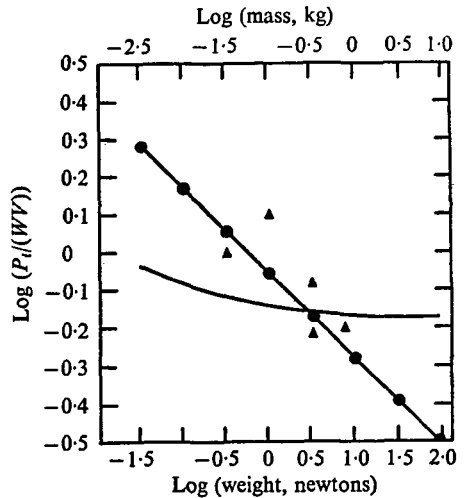

Fig. 3

Fig. 4

Fig. 3. The metabolic rates of a laughing gull with different body masses flying at 10·8 m/s as predicted by measurements (beaded line, $P_i = 36·4\ m^{0·325}$, equation (10)), and by Pennycuick's theory (plain line). The equation $P_i = 103\ m^{1·39}$ fits the line predicted by Pennycuick's theory within better than 1 %. The exponents in the equations for the two lines differ significantly.

Fig. 4. The logarithm of the minimum cost of transport for flying birds of different weights as predicted by metabolic measurements (beaded line, equation (11)) and by Pennycuick's theory (plain line). For the latter curve, values for wing span and equivalent flat plate areas were calculated from equations (7) and (4). The triangles indicate measurements on birds and bats flying in wind tunnels (Table 2).

le modifications increase the complexity of the theory, they also introduce factors that, judging from aerodynamic and physiological data, should be accounted for in a theoretical treatment of flight energetics. In the following sections, I shall show the origin of the power terms in the theory, modify these terms and add some new ones, and adjust the parameters of the modified theory to an optimum fit with the empirical data.

AERODYNAMIC RELATIONS

Reference system and aerodynamic conventions

Unless otherwise noted, force and velocity vectors in this paper are measured relative to a two-dimensional, orthogonal co-ordinate system on the bird's body exclusive of the wings. Since flight is assumed to be horizontal, one axis of the co-ordinate system is vertical, and it, together with the other axis and the axis of the bird's body, lies in a single plane. The bird's body is taken as stationary relative to moving air, and air velocity (V) refers to a horizontal vector measured in the undisturbed air flow in front of the bird unless otherwise noted.

The aerodynamic quantities used are conventional and are described in a variety of textbooks such as Goldstein (1965), Prandtl & Tietjens (1957), and von Mises (1959).

Production of aerodynamic forces by avian wings

The wings in level flight produce a mean aerodynamic force that balances two force vectors: weight, which is vertical, and body drag, which is horizontal. This mean force is conventionally resolved into the orthogonal components lift and thrust. The beating wings generate these forces by changing the momentum of the air in their vicinity. Thrust is generated as the wings accelerate air backwards, and lift is generated as air is accelerated downwards.

The motions of birds' wings are similar to those of a pair of co-axial, counter-rotating propellers or helicopter rotors (Fig. 5). During downstroke each wing is analogous to one blade of the pair of propellers or rotors, and during upstroke it is analogous to a blade of the other. One wing plays the role of first one propeller or rotor blade and then the counter-rotating one by twisting axially between upstroke and downstroke. Unlike the situation with propellers the magnitudes of the aerodynamic forces generated by the wings will differ during downstroke and upstroke.

Because flapping wings, unlike rotors, do not rotate through 360°, they also are similar to the fixed wings of conventional aircraft. The inner part of the flapping wing is primarily a lifting device, for it has a relatively small component of vertical motion and can produce a continuous upward force throughout the stroke cycle. The similarities between flapping wings, helicopter rotors and fixed wings are useful, because they allow the analysis of the energetic requirements of flapping flight to be made in terms of existing theories for helicopters (for example, see Shapiro, 1955) and fixed-wing aircraft. I shall now show how these theories are connected.

First, consider the power transferred to the air in the vicinity of a helicopter in vertical ascent or descent. It is assumed that: (1) the air is accelerated equally at all points on the disc in which the rotor rotates; (2) only axial, rather than rotational, kinetic energy is imparted to the air; and (3) there is no air friction. Thus, the air
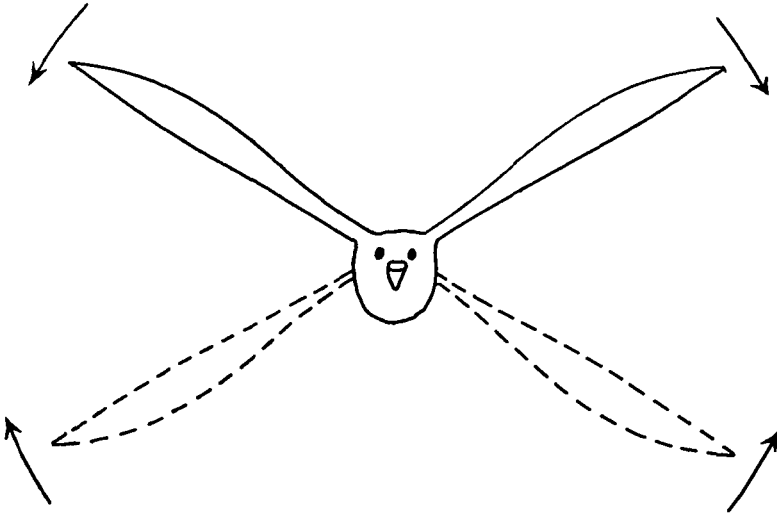
Fig. 5. The wings of a bird during downstroke (plain lines) and upstroke (dashed lines). The leading edges of the wings are drawn as straighter lines than the trailing edges, and the arrows show the directions of wing tip movement. The similarity between the wings and a pair of counter-rotating propellers can be seen if one wing during downstroke and the opposite wing during upstroke are viewed as blades of a single propeller.
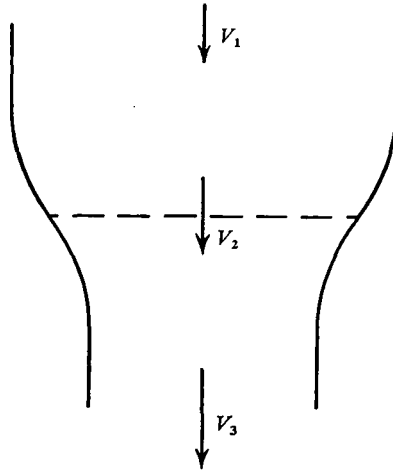

Fig. 6. An actuator disc (dashed line) and the stream of air flowing through it (plain lines). The lengths of the arrows are proportional to the speed of the air approaching the disc from far upstream (V_1), passing through the disc (V_2) and leaving the disc far downstream (V_3). The stream contracts because air is accelerated at the disc.

behaves as if it were accelerated uniformly at the disc in which the rotor rotates (the actuator disc, Fig. 6). Since the power output of the actuator disc to produce lift is the rate at which kinetic energy is added to the air,

$$P_o = m(V_3^2 - V_1^2)/(2t), \tag{12}$$

or, since

$$m/t = \rho S_d V_2, \tag{13}$$

here S_d is the area of the actuator disc,

$$P_o = \rho S_d V_2 (V_3^2 - V_1^2)/2. \tag{14}$$

Also

$$S_d = \tfrac{1}{4}\pi b^2. \tag{15}$$

A similar relation can be derived for a fixed-wing aircraft in horizontal flight. In this case, the air velocity approaching the aircraft has no vertical component ($V_1 = 0$), the air passing through some area S in the vicinity of the wings has the horizontal velocity V_2, and the air leaving the vicinity of the wings has a vertical velocity component V_3. Thus, the rate at which kinetic energy is added to the air to produce lift is (from equation (14)),

$$P_o = \rho S V_2 V_3^2/2. \tag{16}$$

What is the value of the area S? It can be determined from an expression for the *induced drag* (D_{in}) of the wing. Power by definition is the scalar produce of drag and velocity, and the induced drag is the ratio of the power given by equation (16) to the velocity V_2:

$$D_{in} = \rho S V_3^2/2. \tag{17}$$

The induced drag can be described in terms of V_2, for the lift (L) generated by a wing is the rate of change of vertical momentum of the air, or

$$L = \rho S V_2 V_3. \tag{18}$$

Combining equation (17) and (18) yields

$$D_{in} = L^2/(2\rho S V^2), \tag{19}$$

in which the subscript of V_2 has been dropped.

The value of S can now be determined from Prandtl's wing theory (Prandtl & Tietjens, 1957). This theory shows that the induced drag of a wing is least when the wing has an elliptical distribution of lift along its span, and in this case S is equal to the area of a disc with a diameter equal to the wing span (b). That is, the area S for a fixed wing with an elliptical lift distribution is the same as the area S_d of an actuator disc for a helicopter rotor of the same span. Thus, for both the helicopter in vertical flight, and the fixed-wing aircraft in horizontal flight, the mass of air that takes part in the change of momentum is that which flows through a great circle of a sphere of diameter b. Helicopter theory assumes that this great circle relation holds for vertical flight and for flight at all angles between vertical and horizontal (Shapiro, 1955). Because of the similarities of flapping wings to both rotors and fixed wings it is reasonable to assume that the great circle relation also holds for flapping flight, as Pennycuick has pointed out.

POWER OUTPUT TERMS

Induced power

When a helicopter is flying horizontally and not too slowly, the speed (V_2) of air flow through the actuator disc is nearly equal to the forward speed of the helicopter. The induced vertical speed (V_1) is small so that the power equation (14) for the helicopter becomes identical to that (16) for a fixed-wing aircraft. Thus, when the wings have an elliptical lift distribution or act as an actuator disc, the power expended

by a helicopter in forward flight, by a fixed-wing aircraft or by a flying bird accelerate air downward and create lift is given by

$$P_{o,in} = VD_{in} = 2L^2/(\pi\rho b^2 V). \tag{20}$$

This power will be referred to as induced power and is the same as the induced power in Pennycuick's theory.

However, the power calculated from equation (20) represents a minimum for a given situation and might not be achievable in practice. It was derived for the helicopter rotor on the assumption that the acceleration was the same at every point on the actuator disc and was only in the axial direction. These assumptions are not strictly true. Likewise, equation (20) when applied to fixed wings describes induced power only if the lift distribution along the wing is elliptical. For wings with a non-elliptical lift distribution, the correction factor R is introduced into equation (20), yielding

$$P_{o,in} = 2W^2/(\pi\rho b^2 RV). \tag{21}$$

Weight (W) has been substituted for L in this equation since weight and lift are equal in horizontal flight.

R is 1·0 for wings with elliptical lift distribution and is usually in the vicinity of 0·90 to 0·95 for wings actually used for monoplanes. Similar values for R can be calculated for helicopter rotors (Gessow & Myers, 1952). In addition, the wing span of birds when measured from wing tip to wing tip is not the effective span because it includes the width of the body, which is not a lifting area. The body width of birds of various sizes (to be described later) is on the average 13 % of the total wing span. Thus, taking R as 0·9, the total correction factor (R') for wing span that I shall use in this study is

$$R'b^2 = 0\cdot9(0\cdot87b)^2 = 0\cdot7b^2, \tag{22}$$

or

$$R' = 0\cdot7 \tag{23}$$

and

$$P_{0,in} = 2(mg)^2/(\pi\rho b^2 R'V). \tag{24}$$

Pennycuick's theory tacitly assigns R' a value of 1·0, and this change in the value of R' is my first modification to his theory. Weis-Fogh's (1972) analysis of a hovering hummingbird includes details of a wing shape and motion, and leads to an R' value of 0·5, somewhat lower than the R' value that I have chosen.

Parasite power

The preceding section has accounted for the induced power expended in accelerating an air mass vertically to produce lift, but what about the power that is expended in accelerating an air mass horizontally to produce thrust? Thrust in level, unaccelerated flight overcomes the drag (parasite drag) of the body exclusive of the wings, and has the same magnitude as parasite drag but the opposite direction. The parasite power is simply the product of the parasite drag and the velocity of the bird's body through the air.

Parasite drag is given by

$$D = \rho V^2 S C_D/2, \tag{25}$$

where S is a surface area and C_D is the parasite drag coefficient. Values for C_D can be determined in a wind tunnel. To avoid the necessity of measuring S, the product

$\times C_D$ rather than C_D itself is sometimes calculated from wind-tunnel measurements. This product is referred to as the 'equivalent flat plate area' (A) since C_D for a flat plate mounted perpendicular to the air stream is approximately 1·0. Thus, parasite power is given by

$$P_{o, \text{par}} = A\rho V^3/2. \tag{26}$$

This is the equation used in Pennycuick's theory, where A is estimated by equation (4). I will make a second modification to the theory by using an estimate of A based on additional measurements (to be described later) and by incorporating effects of Reynolds number.

The parasite drag coefficient is a function of Reynolds number (Re), given by

$$(\text{Re}) = \rho l V/\mu, \tag{27}$$

where l is some characteristic length of the body under consideration, and μ is the viscosity of air. The ratio ρ/μ in this study has the value 65 200. For objects shaped like bird bodies the parasite drag coefficient decreases as (Re) increases over the appropriate range for specific conditions. Accordingly, the equivalent flat plate area of a bird flying at different speeds should be adjusted as (Re) changes. Pennycuick's theory does not include (Re) effects.

The functional relation between parasite drag coefficient and (Re) has not been investigated for actual bird bodies. As an estimate, I shall assume that this relation has the same form as that for the drag coefficient of an infinitely thin flat plate oriented parallel to the direction of air flow. This assumption is accurate for stream-lined bodies in wind tunnels since the drag of such bodies arises mainly from skin friction (Goldstein, 1965). The drag coefficient of a plate is proportional to (Re) raised to a power between $-\frac{1}{2}$ and $-\frac{1}{5}$, depending on whether the boundary layer is laminar or turbulent, respectively (Goldstein, 1965). The boundary layer of a bird body might be laminar in some places and turbulent in others, depending on body size and the roughness of the feathers (Tucker, 1972). I shall assume that the parasite drag coefficient for bird bodies varies in proportion to (Re) raised to the power $-\frac{1}{2}$, corresponding to a laminar boundary layer.

Parasite power can be expressed in terms of (Re) effects in the following manner for a particular bird. Since

$$C_D = K(\text{Re})^{-\frac{1}{2}} = K'V^{-\frac{1}{2}}, \tag{28}$$

and

$$A = SK'V^{-\frac{1}{2}}, \tag{29}$$

$$K' = A_0 V_0^{\frac{1}{2}}/S, \tag{30}$$

where A_0 is the equivalent flat plate area for a particular bird measured at speed V_0 in the wind tunnel. Combining (29) and (30)

$$A = \frac{A_0 V_0^{\frac{1}{2}}}{V^{\frac{1}{2}}} \tag{31}$$

and

$$P_{o, \text{par}} = \rho A_0 V_0^{\frac{1}{2}} V^{\frac{5}{2}}/2 \tag{32}$$

Profile power

In the preceding treatment of aerodynamic forces generated by a change in momentum, I have assumed that the air is an ideal fluid and exerts no frictional forces or pressure drag on the rotor of wing that moves it. Actual air is viscous and will exert frictional forces and pressure drag. Profile drag comprises these forces, and the power required to overcome them is the profile power.

Profile power cannot be calculated accurately for birds because of uncertainties in the motions and aerodynamic characteristics of bird wings. Each region of the wings is exposed to an air velocity (relative to the wing region) which varies with time, and which at a given time is different for different regions of the wing (see Cone (1968) for a detailed description). In addition, the drag of each wing region depends on the air velocity relative to that region, the shape of the region and the angle of attack of the region relative to the air velocity. Profile power is the integral over space and time of the product of drag and velocity for each region of the wing.

Pennycuick assumes that the profile power is independent of flight speed and estimates it to be proportional to the minimum sum of induced and parasite power. He chooses a proportionality constant of 2 for his calculations and indicates how the results would differ if other constants were chosen. As a third modification to his theory, I shall assume that the profile power varies with flight speed and is proportional to the sum of parasite power and induced power at any given speed. The rationale for this assumption is that the wings expend power to overcome increased parasite and induced drag by increasing the momentum added to the air passing through the great circle previously described. This momentum increase can be accomplished either by moving the wings faster or by increasing their angles of attack. In either case profile drag and profile power will increase. There is no reason why the relation between profile power and the sum of induced and parasite power should be a proportional one, but without additional information this is the simplest assumption.

An additional factor that I shall take into account when calculating profile drag is Reynolds number, which influences both the lift and profile drag coefficients of the wings. Typically, over the range of Reynolds number in which bird wings operate, the ratio C_L/C_D increases as (Re) increases (Feldmann, 1944; Goldstein, 1965; Schmitz, 1960). As C_L/C_D increases, the wings can add a given amount of momentum to the air with a decreasing loss of energy through profile drag. Consequently, the proportionality factor for the relation described in the previous paragraph must be a function of C_L/C_D, and hence of (Re). Thus,

$$P_{o,\mathrm{pr}} = f(\mathrm{Re})(P_{o,\mathrm{par}} + P_{o,\mathrm{in}}), \tag{33}$$

where $f(\mathrm{Re})$ indicates some function of (Re).

Unfortunately, $f(\mathrm{Re})$ is unknown for flying birds, so I will assume that it has the form

$$f(\mathrm{Re}) \propto (\mathrm{Re})^c. \tag{34}$$

There is no particular justification for this assumption other than that the function is a simple one and has the same form as that relating the parasite drag coefficient of a flat plate to (Re). Next, I assume that the characteristic length l for (Re) (which

the width of the wing when (Re) is calculated in connexion with profile drag) is related to body mass by

$$l \propto m^{\frac{1}{3}}. \tag{35}$$

Also, I assume that

$$(\text{Re}) \propto lV. \tag{36}$$

This assumption might seem inappropriate, since the velocity variable is the flight velocity, and a single (Re) value for the wings should be derived from a velocity measured relative to the wings and integrated over space and time. However, if the wings of all birds are assumed to have a constant advance ratio (von Mises, 1959), the integrated velocity and the flight velocity will be proportional, which is all that is required. Even if the advance ratio varies over reasonable values for different birds, the changes in (Re) will turn out to have a trivial effect on values calculated for $f(\text{Re})$. Combining equations (34), (35) and (36) yields

$$f(\text{Re}) = Fm^{\frac{1}{3}c}V^c \tag{37}$$

and

$$F = f(\text{Re}_0)/(m_0^{\frac{1}{3}c}V_0'^c), \tag{38}$$

where F is a proportionality constant and $f(\text{Re}_0)$ is the value of $f(\text{Re})$ at the particular value m_0 and V_0'. Thus,

$$P_{o,\text{pr}} = Fm^{\frac{1}{3}c}V^c(P_{o,\text{par}} + P_{o,\text{in}}). \tag{39}$$

Constants will be assigned to the values of c and F to make the modified version of Pennycuick's theory fit the empirical data as closely as possible.

INTERNAL POWER EXPENDITURE

The power outputs of induced, parasite and profile power represent the rate at which work is done on the air surrounding the bird. The total power input to the bird must cover this work rate plus whatever losses occur in the power train between the point where energy is made available from fuel and the point where it is transferred to the air as work. For example, the mechanical work done by the flight muscles need not be transferred totally to the air. Some of this work increases the kinetic and potential energy of the wings and body during part of the wing-beat cycle and might be degraded to heat within the wings and body during another part of the wing-beat cycle (for details, see Cavagna, Saibene & Margaria, 1964; Weis-Fogh, 1972). An additional amount of work might be degraded to heat in overcoming viscosity and the friction of joints. I shall assume that the rate at which the wings do work on the air is 20% of the metabolic rate of the flight muscles. *In vitro*, vertebrate muscles convert up to 35% of their metabolic energy to mechanical work (Hill, 1939; Woledge, 1968), so I am assuming that less than half of the energy output of avian flight muscles is degraded to heat within the body.

Additional power is consumed for maintenance metabolism, circulation of the blood and ventilation of the respiratory system. I assume that the power for maintenance is the basal metabolic rate and will estimate the power outputs for circulation and respiration in the following sections. I also assume that the heat resulting from various losses within the body allows thermoregulation to be accomplished solely by the regulation of heat loss with no additional heat production.

Pennycuick assumes that the efficiency of the flight muscles is 20% as I do, and that the total additional power expenditure is the basal metabolic rate. The addition of power terms for circulation and respiration is my fourth and final addition to his theory.

Power expenditure of the heart

The power output of the heart is given by

$$P_{o,h} = \dot{Q}(\Delta p_s + \Delta p_{pu}) + \tfrac{1}{2}\rho\dot{Q}[(U_{a,s}^2 - U_{v,s}^2) + (U_{a,pu}^2 - U_{v,pu}^2)], \tag{40}$$

where $\dot{Q}$ is cardiac output, Δp_s is the mean pressure difference between the blood entering and leaving the systemic circulation, Δp_{pu} is the mean pressure difference between blood entering and leaving the pulmonary circulation, and U is the mean velocity of arterial and venous blood leaving and entering the heart in the systemic and pulmonary circulation, as indicated by the subscripts. The first term in equation (40) represents power expended to force the blood through the resistance of the blood vessels. The second term represents the power expended to increase the velocity of venous blood to that of arterial blood. The second term works out to less than 0·1% of a flying bird's total power output and is assumed to be zero in the following analysis.

The power input to the heart is

$$P_{i,h} = P_{o,h}/E, \tag{41}$$

where E is the mechanical efficiency of the heart.

Since virtually all of the oxygen consumed by a bird is carried from the heart to the tissues by the aorta, the Fick equation applies, so that cardiac output is given by

$$\dot{Q} = \frac{\dot{V}_{O_2}}{\Delta C}, \tag{42}$$

where $\dot{V}_{O_2}$ is the rate at which the bird consumes oxygen and ΔC is the difference between the oxygen content of arterial and mixed venous blood. The power input of the whole animal (metabolic rate) is proportional to $\dot{V}_{O_2}$:

$$P_i = J\dot{V}_{O_2}, \tag{43}$$

where J is the energy equivalent of oxygen. By combining equations (40)–(43) the fraction of the total metabolic rate that represents the metabolic rate of the heart is

$$\frac{P_{i,h}}{P_i} = \frac{\Delta p_s + \Delta p_{pu}}{J\Delta CE}. \tag{44}$$

Reasonable estimates for the parameters in equation (44) for a flying bird are $\Delta p_s + \Delta p_{pu} = 2\cdot4 \times 10^4\ \mathrm{N/m^2}$ (180 mmHg),

$$J = \frac{20 \times 10^6\ \mathrm{joules}}{\mathrm{m^3 O_2}}, \quad \Delta C = \frac{0\cdot12\ \mathrm{m^3 O_2}}{\mathrm{m^3\ blood}} \quad \text{and} \quad E = 0\cdot2.$$

These estimates yield a value for power input to the heart that is 5% of the power input of the whole bird.

Power expenditure in ventilation

The power input ($P_{i,r}$) for moving air through the respiratory system cannot be estimated as simply as that of the heart, for account must be taken of both velocity and pressure changes. The power input for ventilation in man has been analysed and

various measurements and estimates made. For rates of oxygen consumption 10–20 times the basal rate in man, the power input required for ventilation is estimated to be between 2 and 10% of the total power input (Otis, 1964). Accordingly, for birds in flight, I shall assume that 5% of the total power input goes towards ventilation.

Power expenditure for maintenance

I assume that maintenance power is the basal metabolic rate $(P_{i,B})$ which can be measured directly or calculated from equations.

STATEMENT OF THE MODIFIED THEORY

The modified theory consists of a summation of the power inputs to the different processes that consume power during flight. These processes comprise induced power, parasite power, profile power, basal metabolic rate and power for circulation and respiration. Thus

$$P_i = (P_{o,\text{in}} + P_{o,\text{par}} + P_{o,\text{pr}})/E + P_{i,B} + P_{i,h} + P_{i,r}. \tag{45}$$

Some of the terms in this equation can be combined. Since

$$P_{i,h} + P_{i,r} = 0 \cdot 1 P_i \tag{46}$$

and

$$P_{o,\text{pr}} = Fm^{\frac{1}{3}c}V^c(P_{o,\text{par}} + P_{o,\text{in}}), \tag{47}$$

therefore

$$P_i = 1 \cdot 11[(P_{o,\text{par}} + P_{o,\text{in}})(1 + Fm^{\frac{1}{3}c}V^c)/E + P_{i,B}]. \tag{48}$$

Substituting expressions for $P_{o,\text{in}}$ and $P_{o,\text{par}}$, where

$$P_{o,\text{in}} = 2(mg)^2/(\pi \rho b^2 R'V)$$

from equation (24) and from equation (32)

$$P_{o,\text{par}} = \rho A_0 V_0^{\frac{1}{2}} V^{\frac{5}{2}}/2$$

yields, when $V_0 = 11 \cdot 0$ m/s,

$$P_i = 1 \cdot 11[(2(mg)^2/(\pi \rho b^2 R'V) + 1 \cdot 96 A_0 V^{\frac{5}{2}})(1 + Fm^{\frac{1}{3}c}V^c)/E + P_{i,B}]. \tag{49}$$

Selecting or measuring flight speed (V) and body mass (m) is straightforward, and I have already specified a value of $0 \cdot 2$ for efficiency (E). Wing span (b) can be measured as a maximum span or estimated from equation (7):

$$b = 1 \cdot 1 m^{\frac{1}{3}}.$$

The equivalent flat plate area of the body (A) can be measured in a wind tunnel or estimated from equation (54) (to be justified later):

$$A = 0 \cdot 00334 m^{0 \cdot 66}.$$

Basal metabolic rate $(P_{i,B})$ can be measured or calculated. The following equations have been derived from those presented by Lasiewski & Dawson (1967). For passerines,

$$P_{i,B} = 6 \cdot 15 m^{0 \cdot 724} \tag{50}$$

and for non-passerines

$$P_{i,B} = 3 \cdot 73 m^{0 \cdot 723}. \tag{51}$$

The parameters c and F are to be determined by fitting equation (49) to existing empirical data. In this study, the values that yield the best fit are $c = -0 \cdot 5$ and $F = 1 \cdot 8$. These values will be justified later.

METHODS

Equivalent flat plate area

I measured the drags of bird bodies in a wind tunnel with a one-component strain-gauge flight balance similar to that shown in fig. 6.65 of Gorlin & Slezinger (1964). The wind tunnel (described in Tucker & Parrott, 1970) was run at an air speed (V_0) of 11·0 m/s, and the turbulence intensity was 0·7%. The strain gauges of the flight balance formed a four-arm bridge, and the degree of imbalance of the bridge was determined by integrating voltage over a period of 50 sec with a digital voltmeter. I calibrated the balance in its operating position by attaching weights to it with a thread that ran over a pulley. The relation between the force component applied parallel to the sensitive axis of the balance and the imbalance of the bridge was virtually linear with a bias of less than $1·5 \times 10^{-3}$ N. The imprecision of the balance was less than a standard error of $0·3 \times 10^{-3}$ N.

Since the aerodynamic forces measured in wind tunnels depend to some extent on the particular wind tunnel, I used the balance to measure the drag coefficient of a sphere $25·4 \times 10^{-3}$ m in diameter. Spheres have been used as test objects in wind tunnels by others. The drag coefficient at a (Re) value of 18×10^3 (the diameter of the sphere is the reference length for (Re)) was 0·46, which compares to values of 0·42 and 0·47 measured by others at this (Re) value (Goldstein, p. 495). The drag coefficient of a sphere is

$$C_D = \frac{2D}{\rho V_0^2 a},\tag{52}$$

where a is cross-sectional area. Before calculating the drag coefficient I measured the drag of the vertical rod that attached the sphere to the balance and subtracted the rod drag from the total measured drag. This rod was cylindrical, $3·3 \times 10^{-3}$ m in diameter, and extended 60×10^{-3} m above the streamlined housing of the flight balance.

For measurements on birds, bodies of five birds (white-throated sparrow, *Zonotrichia albicollis*; budgerigar, *Melopsittacus undulatus*; starling, *Sturnis vulgaris*; laggar falcon, *Falco jugger*; mallard, *Anas platyrhynchos*) were weighed, the wings were removed, and the bodies were frozen in a flight-like posture. A hole was drilled in the breast of each frozen body and a wooden plug was inserted and frozen into place. Then the plug was drilled and tapped to receive the rod from the flight balance. The body of the bird on the balance was oriented with respect to the air stream in the wind tunnel in what appeared to be a natural flight attitude. After each measurement, I calibrated the flight balance with the bird body in place.

Wing span and body width

Wing span varies during the stroke cycle, and I measured a maximum value when the wings were horizontal during the downstroke for budgerigars and gulls flying level in a wind tunnel. A remote-controlled camera placed directly behind the birds photographed the birds as they flew. Wing-span measurements made on the photographs and multiplied by a scale factor had a systematic error of less than 2×10^{-3} m and an imprecision estimated to be less than a standard error of 5×10^{-3} m.
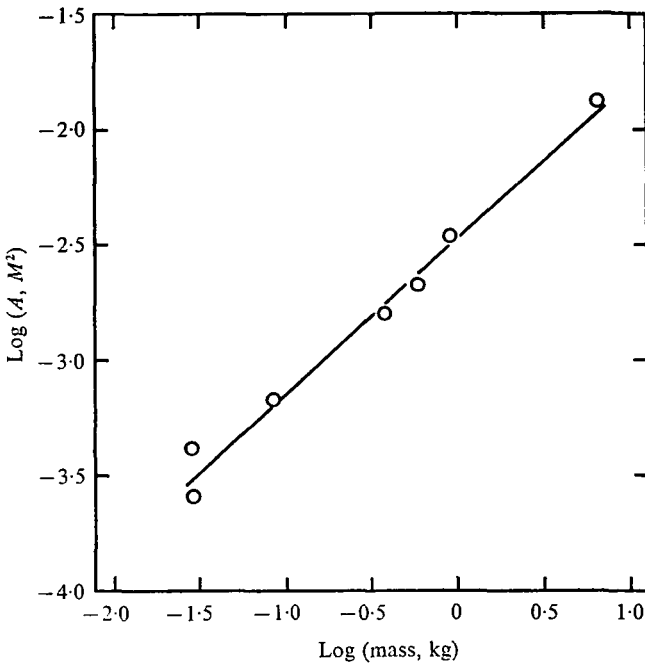
Fig. 7. Wind-tunnel measurements of the equivalent flat plate areas of wingless bodies of birds with different body masses.

I measured the maximum body widths and wing spans of the birds used for body-drag measurements with the exception of the mallard and with the addition of the laughing gull. These measurements were made either on photographs taken in the wind tunnel as described above, or on dead birds with wings held at maximum span. Body width expressed as a percentage of total wing span varied from 9 % (falcon) to 18 % (sparrow), with a mean value of 13 %.

Fitting the modified theory to data

I adjusted the parameters c and F in equation (49) until I obtained values for each that produced the closest simultaneous fit (as determined by eye) of this equation to three sets of measured data: the metabolic rates of the budgerigars and laughing gulls at different flight speeds between 6 and 13 m/s (equations (8) and (9), respectively) and the cost of transport for flying birds with weights between 0·03 and 100 N (3×10^{-3} and 10 kg, equation (11)).

RESULTS

The equivalent flat plate area of bird bodies varied according to the least-squares equation (Fig. 7).

$$\log A = 0.660 \log m - 2.48 \tag{53}$$

(standard error of estimate = 0·0843, N = 7) or
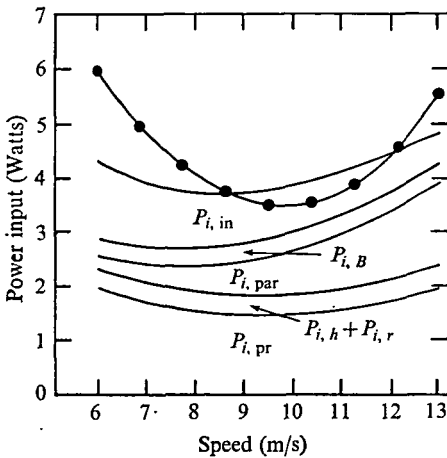
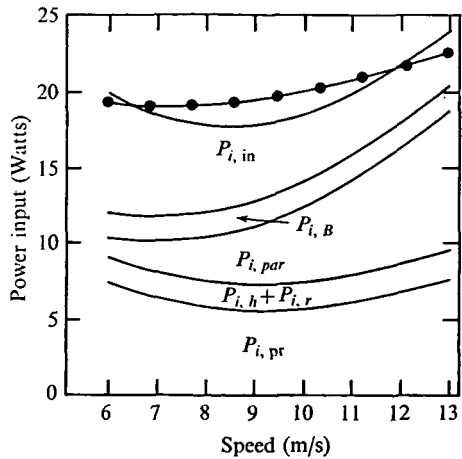$$A = 0.00334 m^{0.660}, \tag{54}$$

Fig. 8

Fig. 9

Fig. 8. The metabolic rates of a budgerigar flying at different speeds as predicted by measurements (beaded line, equation (8)) and by the modified theory (plain line). The power inputs for profile power; respiration and circulation; parasite power; basal metabolism and induced power are shown by partitions. The budgerigar has the characteristics given in the legend of Fig. 1.

Fig. 9. The metabolic rates of a laughing gull flying at different speeds as predicted by measurements (beaded line, equation (9)) and by the modified theory (plain line). The power inputs for profile power; respiration and circulation; parasite power; basal metabolism and induced power are shown by partitions. The gull has the characteristics given in the legend of Fig. 2.

where m is the mass of the intact bird. These equations are fitted to the data from the five species used in this study, the pigeon (*Columba livia*, Pennycuick, 1968) and Ruppell's griffon vulture (*Gyps ruppellii*, Pennycuick, 1971).

The modified theory fits the empirical data most closely when c and F are assigned values of -0.5 and 1.8, respectively (Figs. 8, 9). The parameters used for the budgerigar and the gull (Table 2) in the modified theory were measured or calculated from data on other birds. The measurements show that both budgerigars and laughing gulls are atypical in that for their masses budgerigars have short wings and a small equivalent flat plate area, while laughing gulls have long wings.

The sensitivity of the modified theory to changes in various parameters depends on the values of the parameters. As an example, the percentage changes in power input that result from a 5% increase of one parameter at a time are shown in Table 3 for a bird with a mass of 0.1 kg flying at 9.5 m/s.

The modified theory accounts for the variation in cost of transport with body mass more accurately than does Pennycuick's theory. This improvement is largely due to allowing parasite and profile power to vary with Reynolds number. If these power terms are not allowed to vary with Reynolds number, the cost of transport of the modified theory varies with body mass in about the same way as predicted by Pennycuick's theory (Fig. 10).

Neither Pennycuick's theory nor the modified theory predict accurately the measured variation of power input with body mass in the flying gull (Fig. 11), although the modified theory offers a slight improvement.

Table 2. *Parameters and predictions for various flying animals*

	Budgerigar, *Melopsittacus undulatus*	Laughing gull, *Larus atricilla*	Fish crow, *Corvus ossifragus*	Greater spearnosed bat, *Phyllostomus hastatus**	Flying fox, *Pteropus gouldii**
Mass, kg	0·035	0·322	0·275	0·0927	0·780
Wing span, m					
Measured	0·235	0·930	0·600*	0·45	1·17
Predicted†	0·360	0·754	0·715	0·498	1·01
Equivalent flat plate area, m²					
Measured	0·258 × 10⁻³	—	—	—	—
Predicted‡	0·365 × 10⁻³	1·58 × 10⁻³	1·43 × 10⁻³	0·695 × 10⁻³	2·84 × 10⁻³
Flight speed,§ m/s	10·7	13·0	11	8·0	9·9
Metabolic rate, Watts					
Basal	0·330||	1·64||	2·42¶	0·668||	3·12||
Measured in flight**	3·70	24·5	24·8	9·08	47·1
Predicted by modified theory**	4·06	22·3	26·0	7·58	47·7
% error	+9·7	−9·0	+4·8	−16·5	+1·3
Predicted by Pennycuick's theory**	4·23	24·3	29·5	7·24	57·5
% error	+14·3	−0·8	+19·0	−20·3	+22·1

* Personal communication, S. P. Thomas.   † Equation (7).   ‡ Equation (54).
§ Speed where measured P_i/V is minimum.   \|\| Equation (51).
¶ Equation (50).   ** At tabled speed value.

Table 3. *Percentage changes in P_i when the indicated parameters of the modified theory are increased by 5%, one at a time*

(P_i evaluated for a bird with a mass of 0·1 kg flying at 9·5 m/sec.)

b	E	F	A	$P_{i,h}+P_{i,r}$	c
−3·60	−4·29	+2·08	+2·57	+0·46	+0·61

The modified theory and Pennycuick's theory are in fair agreement in their predictions of power inputs for medium-size birds, but Pennycuick's theory yields lower values for small birds and higher values for large birds (Fig. 12).

Additional data on metabolic rates during flight have become available for bats (S. P. Thomas, unpublished) and for a crow (Bernstein, Thomas & Schmidt-Nielsen, 1973) since the greater part of this paper was written. Comparisons between measured values of metabolic rates at various speeds and predictions from both Pennycuick's theory and the modified theory are shown in Table 2 and Fig. 13. The data for the crow has been fitted by linear least-squares with the equation

$$P_i = 0·611V + 18·1, \tag{55}$$

which describes the means reported for level flight by Bernstein *et al.* within 1·5% or better.

The modified theory fits the available data for metabolic rates in flight better than Pennycuick's theory when metabolic rates are measured at the speeds where the ratio P_i/V is minimum (Table 2). The mean absolute value of the deviations of the predictions from the measurements is 8·3% (S.D. = 5·72) for the modified theory and 15·3% (S.D. = 8·60) for Pennycuick's theory.
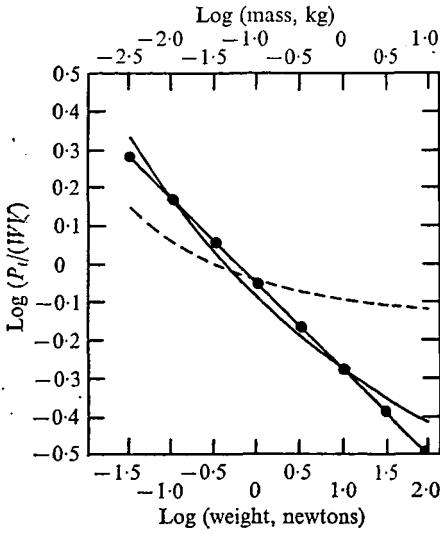
Fig. 10

Fig. 11

Fig. 10. The logarithm of the minimum cost of transport for flying birds of different weights as predicted by metabolic measurements (beaded line, equation (11)) and by the modified theory (plain line). For the latter curve, values for wing span and equivalent flat plate area were calculated from equations (7) and (54). The dependence of minimum cost of transport on body weight is largely due to Reynolds number effects. This can be seen from the dashed line, which was calculated from the modified theory on the assumption that both parasite and profile power were independent of Reynolds number.
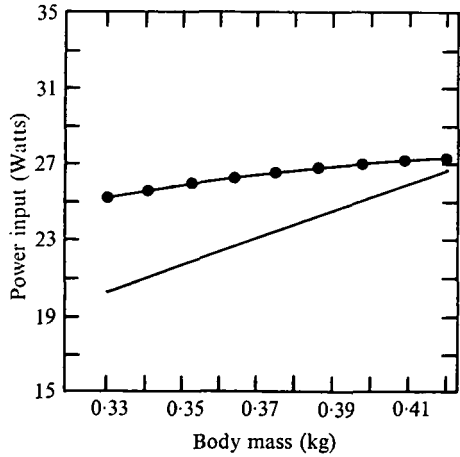
Fig. 11. The metabolic rates of a laughing gull flying at 10·8 m/s with different body masses as predicted from measurements (beaded line, $P_i = 36·4m^{0·325}$, equation (10)), and by the modified theory (plain line). The equation $P_i = 70·6m^{1·11}$ fits the line predicted by the modified theory within better than 1%. The exponents in the equations for the two lines differ significantly.

ESTIMATING EQUATIONS

Equation (49) is tedious to solve without automatic computing equipment. Some of its solutions can be described approximately by means of equations that are quickly soluble with a slide rule. I have used least-squares fitting techniques to derive the following approximate equations.

For minimum cost of transport,

$$P_i/(WV) = 0·927W^{-0·20}. \tag{56}$$

This equation yields results that, compared to those from equation (49), are 11% low at a weight of 0·03 N, 9% high at a weight of 1 N and 11% low at a weight of 100 N.

For total power input at the speed where cost of transport is minimum, and when wing span is given by equation (7),

$$P_i = 84·7m. \tag{57}$$

This equation yields results that, compared to those from equation (49) are 5% low at 0·003 kg, 9% high at 0·1 kg and 10% low at 10 kg. For birds with wing spans 20% greater than that given by equation (7),
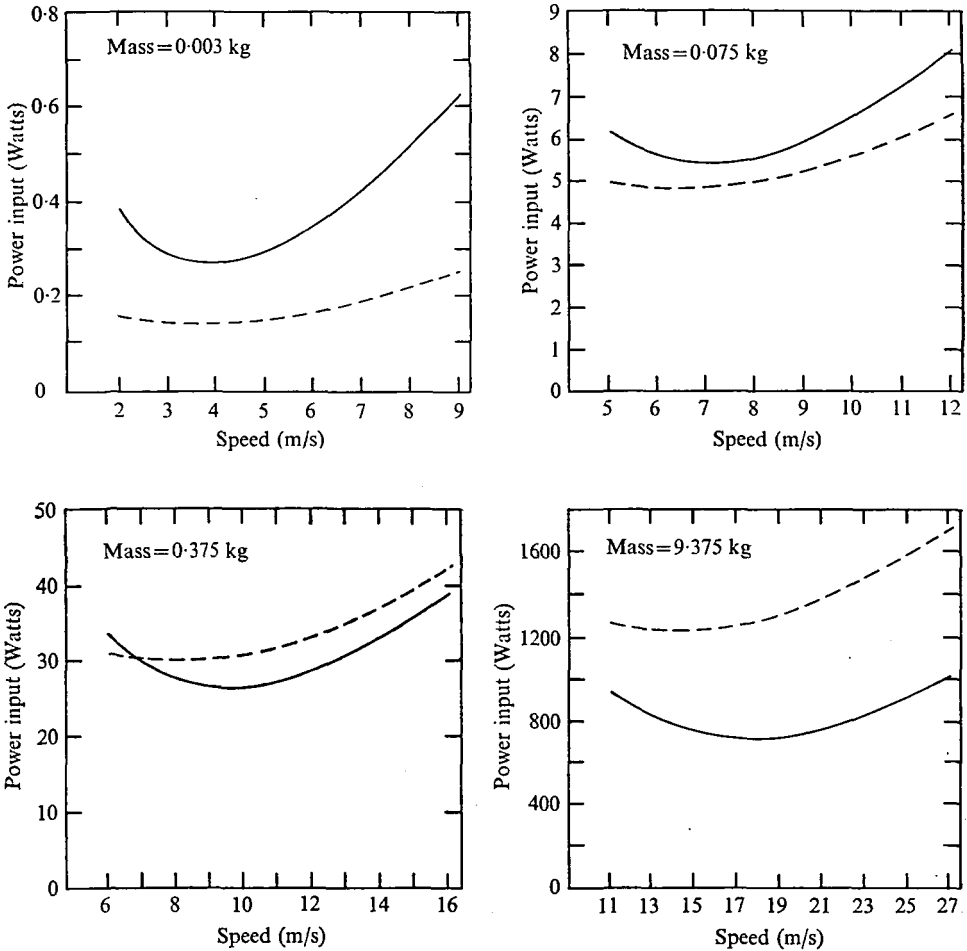
$$P_i = 67·3m \tag{58}$$

Fig. 12. Curves of metabolic rate versus speed for non-passerine flying birds of various sizes as calculated from the modified theory (plain lines) and from Pennycuick's theory (dashed lines). Wing spans and equivalent flat plate areas were calculated for the modified theory from equations (7) and (54), and for Pennycuick's theory from equations (7) and (4).

and for birds with wing spans 20% shorter,

$$P_i = 113m. \tag{59}$$

The flight speeds at which cost of transport is minimum are given by

$$V = 14 \cdot 6m^{0 \cdot 20} \tag{60}$$

for birds with wing spans described by equation (7). Equation (60) yields results that, compared to those from equation (49) are 5% high at 0·003 kg, and within 1% or better from 0·01 to 10 kg. For birds with wing spans 20% greater than that given by equation (7),

$$V = 13 \cdot 1m^{0 \cdot 21} \tag{61}$$

and for birds with wing spans 20% shorter,
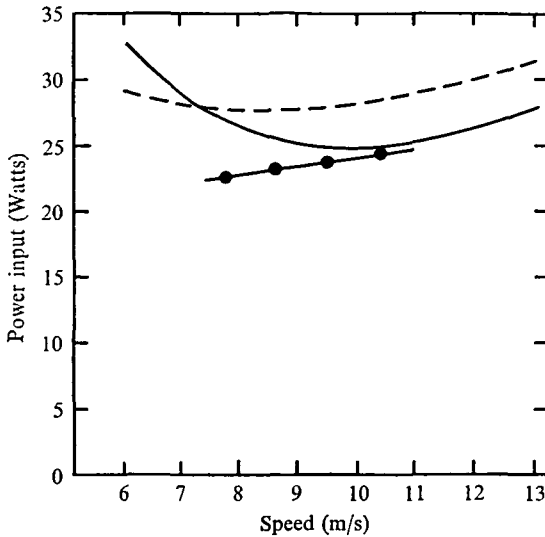
$$V = 16 \cdot 7m^{0 \cdot 20}. \tag{62}$$

Fig. 13. The metabolic rate of a fish crow (*Corvus ossifragus*) flying level at different speeds as determined from measurements (beaded line, equation (55)), Pennycuick's theory (dashed line) and the modified theory (plain line). The crow has a mass of 0·275 kg, a wing span of 0·60 m (personal communication), and (since it is a passerine) a basal metabolic rate given by equation (50).

SUMMARY

1. Pennycuick's (1969) theory for the energetic requirements of avian flight predicts the metabolic rates of budgerigars and laughing gulls flying level at intermediate speeds in a wind tunnel with an accuracy of 10 % or better. However, its predictions appear to be low for most birds with masses less than 0·1 kg and high for most birds with masses greater than 0·5 kg.

2. Four modifications are made to Pennycuick's theory: (1) a different computation of induced power; (2) a different estimate of equivalent flat plate area that includes Reynolds number effects, and is based on additional measurements; (3) a different estimate of profile power that includes Reynolds number effects; and (4) the addition of power terms for respiration and circulation. These modifications improve the agreement between the theoretical predictions and existing measurements for flying birds and bats.

3. The metabolic rates of birds and bats in level flight at various speeds can be estimated by the modified theory if body mass alone is measured. Improved estimates can be made if wing span is measured as well. In the latter case the theory predicts measured values with a mean absolute error of 8·3 %.

4. The results of the modified theory are presented by approximate equations that can be solved quickly for metabolic rate and flight speed with a slide rule.

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