METABOLISM DURING FLIGHT IN TWO SPECIES OF BATS, *PHYLLOSTOMUS HASTATUS* AND *PTEROPUS GOULDII*

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SUMMARY

The energetic cost of flight in a wind-tunnel was measured at various combinations of speed and flight angle from two species of bats whose body masses differ by almost an order of magnitude. The highest mean metabolic rate per unit body mass measured from *P. hastatus* (mean body mass, 0·093 kg) was 130·4 W kg^{-1}, and that for *P. gouldii* (mean body mass, 0·78 kg) was 69·6 W kg^{-1}. These highest metabolic rates, recorded from flying bats, are essentially the same as those predicted for flying birds of the same body masses, but are from 2·5 to 3·0 times greater than the highest metabolic rates of which similar-size exercising terrestrial mammals appear capable. The lowest mean rate of energy utilization per unit body mass *P. hastatus* required to sustain level flight was 94·2 W kg^{-1} and that for *P. gouldii* was 53·4 W kg^{-1}. These data from flying bats together with comparable data for flying birds all fall along a straight line when plotted on double logarithmic coordinates as a function of body mass. Such data show that even the lowest metabolic requirements of bats and birds during level flight are about twice the highest metabolic capabilities of similar-size terrestrial mammals. Flying bats share with flying birds the ability to move substantially greater distance per unit energy consumed than walking or running mammals. Calculations show that *P. hastatus* requires only one-sixth the energy to cover a given distance as does the same-size terrestrial mammal, while *P. gouldii* requires one-fourth the energy of the same-size terrestrial mammal. An empirically derived equation is presented which enables one to make estimates of the metabolic rates of bats and birds during level flight in nature from body mass data alone. Metabolic data obtained in this study are compared with predictions calculated from an avian flight theory.

INTRODUCTION

Vertebrate flight is interesting from both an evolutionary and physiological viewpoint. Although mammals and birds have evolved from two distinct reptilian stocks, representatives from both taxonomic classes have gained access to the skies by finding solutions to the aerodynamic prerequisites associated with this elite form of animal locomotion.

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Associated with the aerodynamic requirements are the energetic demands of flight. Data from flying birds (Tucker, 1968, 1972; Bernstein, Thomas & Schmidt-Nielsen, 1973) show that these animals consume energy at rates that are more than twice those of similar size terrestrial mammals undertaking heavy exercise (Pasquis, Lacaisse & Dejours, 1970). Although birds possess a number of anatomical and physiological adaptations for flight which are not shared by mammals, measurements obtained from the bat *Phyllostomus hastatus* during tethered flight show this species is capable of consuming oxygen at a rate comparable to that of a flying bird (Thomas & Suthers, 1972).

The experimental approach employed in the above study on bats had two main shortcomings: (1) the investigators had no control over the speed at which the tethered bats flew, and (2) metabolic measurements were restricted to flights along a circular flight path. Wind-tunnel studies on birds show the energetic cost of flight is a function of speed as well as flight angle (Tucker, 1968).

In the following investigation I have measured the energetic cost of flight at various combinations of speed and flight angle from two species of bats whose body masses differ by almost an order of magnitude. These data are discussed in relation to those available for flying birds to learn what similarities and differences exist in the energetic cost and effectiveness of aerial locomotion in these two independently evolved groups of flying vertebrates. Metabolic data from flying bats are also discussed in relation to those for exercising terrestrial mammals to compare the energetic cost and effectiveness of these two forms of mammalian locomotion.

MATERIALS AND METHODS

Units and accuracy

The International System of Units (see Mechtly, 1969) based on the metre, kilogram and second has been used throughout this paper. The newton (N) can be converted to kilograms force by multiplying by 0·102. The cubic metre volume unit can be converted to litres by multiplying by $1·0 \times 10^3$. The watt (W) power unit can be converted to kilocalories per hour by multiplying by 0·860. Measurements throughout this study were made at air temperatures between 21 and 28 °C. All gas volumes are corrected to a temperature of 0 °C and a pressure of $1·013 \times 10^5$ N/m² (760 mmHg).

The accuracies of measurement processes are described in terms of systematic error and imprecision as recommended by Eisenhart (1969) and Ku (1969) using the same arbitrary set of criteria used by Tucker (1972). Thus, imprecision has been called negligible if the standard error of measurements made during an experiment under controlled conditions is less than one-sixth of the systematic error, or if the standard error of measurements made during calibration is one-sixth or less of the standard error of measurements made during an experiment under controlled conditions. Systematic errors have been called negligible if they are less than one-half of the standard errors of measurements made during an experiment under controlled conditions.

Experimental animals

Phyllostomus hastatus (Microchiroptera, Phyllostomidae) is an echolocating omnivorous species with a wing-span of about 0·45 m. Two members of this species were

studied. The smaller individual (bat 1) had a mean body mass of 0·087 kg (S.D. = 1·9 × 1·0^{-3}, N = 75) while that of the larger *P. hastatus* (bat 2) was 0·099 kg (S.D. = 1·5 × 10^{-3}, N = 80). This species was maintained in the laboratory on a diet of ground beef, bananas, melons and a vitamin–mineral supplement (Pervinal).

Pteropus gouldii (Megachiroptera, Pteropidae) is a visually orienting frugivorous species with a wing-span of about 1·2 m. The one *P. gouldii* investigated had a mean body mass of 0·779 kg (S.D. = 0·011, N = 65) and was maintained on bananas, grapes, melons, high-protein baby cereal, and Pervinal.

Wind-tunnel

The bats were trained to fly in the test section of a wind-tunnel of open-circuit design (illustrated in Tucker & Parrott, 1970). Both the upstream and downstream ends of the test section were fitted with a cloth screen (1·3 × 10^{-2} m mesh). The fan was equipped with a variable-speed motor. The long axis of the tunnel could be tilted by an angle (θ) from horizontal to simulate ascending and descending flight. Throughout this study (θ) is defined as being positive in sign when the air velocity vector has a downward component (as during ascending flight), and negative in sign when the air velocity vector has an upward component (descending flight).

The direction and turbulence of the air flow in the region of the test section where a given bat flew were measured at various points on an imaginary grid using methods described by Tucker & Parrott (1970). The yaw-meter could detect 0·1° changes in the direction of air flow. The direction of air flow varied by 1·2° or less in the regions of the test section where the bats flew. Mean values accurate to 0·4° or better have been used in all calculations.

Turbulence was measured with a Disa 55D05 hot-wire anemometer connected to a RMS and DC voltmeter. The mean turbulence was 3% or less in the regions where the bats flew. The RMS voltmeter was accurate to 5% and had a negligible imprecision. The DC voltmeter had both an imprecision and systematic error which were negligible. Air-speed values are based on previous calibrations made on this wind tunnel by Tucker & Parrott (1970), which relate fan RPM to air speed (measured by a pitot-static tube).

Training and behaviour

Both species required about 6 weeks of nightly training in the wind-tunnel before they were capable of long well-coordinated flights while wearing a mask and associated air tube. The animals were first trained to fly while wearing a mask with an open front, to which was eventually attached a flexible vinyl air tube. This training mask was finally replaced with the type of mask used for metabolic measurements.

By the end of the training period all three bats would consistently fly with a mask and air tube at all combinations of air speed and flight angle (θ) examined for periods lasting at least 12 min in duration. Metabolic measurements were made from the two *P. hastatus* over a range of speeds during ascending (θ = +2°) as well as level (θ = 0°) and descending (θ = −2°, −4°) flight, while *P. gouldii* would only fly at level or descending flight angles for periods long enough to insure steady metabolic measurements.

Both the larger *P. hastatus* (bat 2) and *P. gouldii* would maintain an essentially

constant flying position in the centre of the tunnel's cross-section about 0·2 m behind the upwind screen. The lengths of the vinyl tubes which trailed freely from the masks of these individuals to the floor of the test section were 1·02 m (bat 2) and 1·18 m (*P. gouldii*), and had masses of 4·2 × 10⁻³ kg and 1·13 × 10⁻² kg respectively.

The smaller *P. hastatus* (bat 1) consistently flew in the downstream half of the test section and about 0·15 m from the ceiling regardless of whether or not it was flying with a mask and air tube. Bat 1 would only fly for about 5 min at level and ascending flight angles at speeds above 8 m s⁻¹ when the tube trailed in the air from the mask to the floor of the test section. This problem was overcome by supporting part of this individual's air tube with a ringstand positioned upwind from the flying bat. The ringstand supported the air tube at a point 0·67 m off the tunnel's floor (0·25 m below the plane of the flying bat's body) so that a 0·75 m length of tube (mass = 2·8 × 10⁻³ kg) was suspended in air between the ringstand and the mask of bat 1. This modification enabled bat 1 to fly at all flight conditions examined for periods lasting 12 min or longer.

The flight position of bat 1, relative to the vertical axis of the ringstand, was measured for each flight and was found to remain essentially constant at a given air speed at all flight angles examined. This individual's flight position did vary consistently with air speed in a manner such that at the lowest speed (6·2 m s⁻¹) bat 1 flew almost directly above the ringstand, while at the highest speed (9·0 m s⁻¹) bat 1 would maintain a position at a point 0·4 m downstream from the ringstand's vertical axis.

Flying with a mask and air tube reduced the highest speed at which each of the three unencumbered bats would steadily fly in the level tunnel by about 1 m s⁻¹.

Metabolic measurements

The 2·6 × 10⁻³ kg masks worn by *P. hastatus* during metabolic measurements (Fig. 1) were similar in their basic construction to those described by Thomas & Suthers (1972). The front of each mask was equipped with a thin Mylar membrane which enabled *P. hastatus* to echolocate but prevented the escape of expired gases from the front of the mask. Room air entered the top of the mask through an opening located in the back of an anteriorly directed air scoop. This air together with expired gases was withdrawn from the front of the mask at a rate ($\dot{V}_E$) of 0·1525 × 10⁻³ m³ s⁻¹ (9·15 l min⁻¹) by a flexible vinyl tube (2·7 × 10⁻³ m O.D.) connected to a vacuum and gas analysis system similar to that illustrated by Tucker (1969).

The mask worn by *P. gouldii* was constructed from a flat piece of celluloid formed into a cone and glued to a piece of celluloid centrifuge tube. It had a mass of 5·5 × 10⁻³ kg and was held on the animal by a rubber band (Fig. 2). Room air entered the back of the mask and, together with the animal's expired gases, was withdrawn from the front at a rate of 0·6026 × 10⁻³ m³ s⁻¹ (36·5 l min⁻¹) through a vinyl tube (5·0 × 10⁻³ m O.D.) connected as described above.

Rotameters were calibrated with Vol-U-Meters (Brooks Division, Emerson Electric Company) for the particular pressures at which they were to be used. The systematic error of the flowmeter readings was negligible, and flow rates obtained during calibration ($N = 5$) were within 3% of the mean value used in calculations.

Fig. 1. *Phyllostomus hastatus* flying in a wind-tunnel while wearing a mask (described in text) which allowed orientation pulses to be transmitted through the mask during echolocation.

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Fig. 2. *Pteropus gouldii* flying in a wind-tunnel while wearing a celluloid mask.

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The paramagnetic oxygen analyser (Beckman G-2, equipped with a back pressure regulator) gave a 0·25 m deflexion for a change of 0·005 in fractional concentration of oxygen, and was calibrated by changing the total pressure of air flowing through its paramagnetic sensing unit. The infra-red carbon dioxide analyser (Beckman, model 215) was calibrated using the null balance method described by Tucker (1972), except that carbon dioxide was infused into the empty mask directly from a Volu-U-Meter. Both gas analysers had a systematic errors and imprecisions that were negligible. Carbon dioxide production was measured simultaneously with oxygen consumption during approximately one-third of the total number of metabolic measurements made from each individual.

A flying bat's rate of oxygen consumption ($\dot{V}_{O_2}$) was calculated from stable recorder readings using Tucker's (1968) equation (2) when carbon dioxide production data ($\dot{V}_{CO_2}$) were available for a given flight. A given bat's mean respiratory quotient ($\dot{V}_{CO_2}/\dot{V}_{O_2}$) was calculated from the above, and substituted in Tucker's equation (3) to compute $\dot{V}_{O_2}$ for flights when only the oxygen analyser trace was recorded. A given individual's rate of oxygen consumption was then converted to watts by multiplying the former value by a RQ-dependent constant (see Results). Five metabolic measurements were made from each individual at each combination of tunnel angle and air speed.

An animal flying with a mask and tube does work at a higher rate, and consequently has a higher metabolic rate than the unencumbered individual flying at the same tunnel angle and speed. The metabolic rate measured from the masked bat can be corrected for the rate of energy expenditure used to overcome forces generated by the mask and tube. This correction can be made by first determining the flying animal's partial efficiency of energy utilization as described below.

Partial efficiency

The partial efficiency (E_p: Kleiber, 1961) of an exercising animal is a ratio that relates the change in rate of work performed (Δ power output, ΔP_0) to the change in metabolic rate (Δ power input, ΔP_i) in going from one level of work to another, or

$$E_p = \Delta P_0/\Delta P_i, \tag{1}$$

where

$$\Delta P_0 = P_{0_1} - P_{0_2} \tag{2}$$

and

$$\Delta P_i = P_{i_1} - P_{i_2}. \tag{3}$$

For the purpose of calculating E_p values for an animal flying in a wind-tunnel, ΔP_i is the change in the animal's metabolic rate which results from tilting the long axis of the tunnel from one angle (θ_1) to another (θ_2) at a constant air speed.

Tucker (1972) has outlined the theoretical basis and general methods that enable one to determine ΔP_0 values, and thus calculate E_p values for an animal flying in a wind-tunnel. The sum of the various forces acting on a flying animal's body must be zero if the animal is to maintain its position in the test section of the tunnel. For the purposes of the present study, I will only be concerned with those force components that act on the flying bat's body along an axis parallel to the direction of

air flow. It follows that these force components must sum to zero during equilibrium flight. For a bat flying with a mask and tube, these components are as follows:

T the thrust produced by the wings,

D_b the aerodynamic drag of the body, excluding the wings,

D_m the difference between the drags of the masked and unmasked bat model,

F_t the total force component produced by the tube that acts along an axis parallel to the direction of air flow. F_t consists of two components: (1) D_t, the aerodynamic drag of the tube, and (2) F_{gt}, the gravitational force component of the tube.

F_b the gravitational force component of the bat's body that acts along an axis parallel to the direction of air flow.

F_m the gravitational force component of the mask that acts along an axis parallel to the direction of air flow.

For convenience, the latter two force components can be summed to give

$$F_{b,m} = F_b + F_m. \qquad (4)$$

By convention, thrust (T) acts in a direction opposite to that of airflow, and the various drag forces (D_b, D_m, D_t) act in the same direction as air flow. Thrust and drag forces are always positive in sign.

The gravitational force components ($F_{b,m}$, F_{gt}) are functions of θ, the angle at which the long axis of the tunnel is tilted from horizontal. Thus, $F_{b,m}$ and F_{gt} act in the direction of drag when the air flow has a downward component (i.e. ascending flight, $\theta > 0°$), are zero when air flow is horizontal (i.e. level flight, $\theta = 0°$), and act in a direction opposite to that of drag when the air flow has an upward component (i.e. descending flight, $\theta < 0°$). By establishing the set of coordinates shown in Fig. 3, the values of $F_{b,m}$ and F_t are defined in a manner consistent with above conventions for thrust and drag forces, and the various equations used in this study.

Thus, the gravitational force component of the bat's body and mask ($F_{b,m}$) is given by the relation

$$F_{b,m} = -W_{b,m} \sin \theta, \qquad (5)$$

where $W_{b,m}$ is the magnitude of the weight of the bat's body plus mask. Similarly,

$$F_{gt} = -W_t \sin \theta, \qquad (6)$$

where W_t is the magnitude of the weight of the tube suspended in air by the flying bat. The total force component exerted by the tube on the flying bat (F_t) is the algebraic sum of the tube's aerodynamic drag (D_t) and gravitational force component (F_{gt}), or:

$$F_t = -D_t + F_{gt}. \qquad (7)$$

Since in equilibrium flight the force components acting on the bat's body along an axis parallel to the direction of air flow must sum to zero, the following equilibrium equation can be written

$$T = D_b + D_m - F_t - F_{b,m}. \qquad (8)$$

One can quantitatively change the amount of thrust the wings of a flying animal
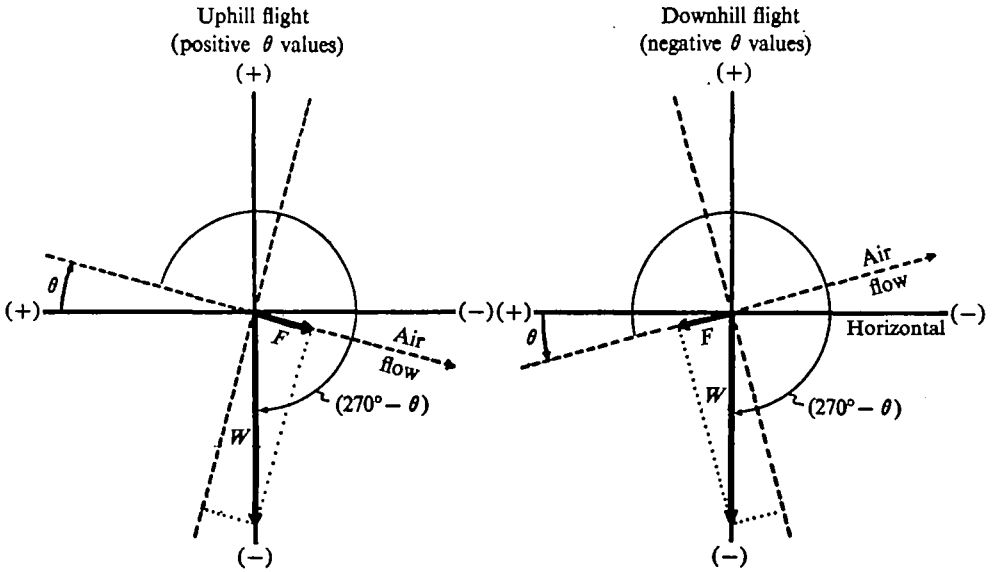
Fig. 3. The relationship between a generalized gravitational force component (F) acting along an axis parallel to the direction of air flow, and the angle (θ) at which the long axis of the tunnel is tilted from horizontal. The value of F is given by the relation $F = -W \sin \theta$, where W is the magnitude of the weight vector. See text for additional details.

must produce at a constant air speed by tilting the tunnel from one angle to another. The change in thrust (ΔT) associated with this change in tunnel angle is given by the relation

$$\Delta T = \Delta D_b + \Delta D_m - \Delta F_t - \Delta F_{b,m}. \tag{9}$$

I assume that ΔD_b and ΔD_m are negligible as the tunnel tilts. Equation (9) can then be written as

$$\Delta T = -\Delta F_t - \Delta F_{b,m}. \tag{10}$$

The rate at which the thrust of the bat's wings does work (Power output, P_0) is by definition the product of the magnitudes of thrust (T) and air speed (V). For an animal flying in a tunnel at a constant V, the change in power output (ΔP_0) associated with a change in θ from one angle to another is given by the relation

$$\Delta P_0 = \Delta T V. \tag{11}$$

The value for ΔP_0 together with the appropriate ΔP_i value is then substituted in equation (1) to calculate the animal's E_p for the particular set of flight conditions under consideration.

Metabolic corrections for mask and tube forces

In the following section I will describe how E_p values, together with a knowledge of the forces generated by the mask and tube, are used to estimate the animal's energetic requirements for unencumbered flight from metabolic data collected from the masked bat.

For equilibrium flight at a particular tunnel angle and speed, the additional thrust

(ΔT) which the wings of a masked bat must produce, relative to the unencumbered individual, is given by the relation

$$\Delta T = T_m - T_u,$$ (12)

where T_m and T_u are the thrusts of the masked and unmasked bat respectively. The equation for T_m is given by substituting equation (4) into equation (8) for $F_{b,m}$ or

$$T_m = D_b + D_m - F_t - F_b - F_m$$ (13)

and the thrust of the unmasked bat is given by the relation

$$T_u = D_b - F_b.$$ (14)

Thus, from equations (12), (13) and (14):

$$\Delta T = D_m - F_t - F_m.$$ (15)

The change in power output (ΔP_0) associated with this change in thrust is then calculated from equation (11). The change in metabolic rate (ΔP_i) associated with this change in power output (ΔP_0) is estimated by substituting the latter value together with the appropriate E_p valve into equation (1), and solving for ΔP_i. Thus

$$\Delta P_i = \Delta P_0 / E_p,$$ (16)

where ΔP_i represents the additional energy a masked bat flying at a particular θ and V must expend, relative to the unmasked bat, to overcome the forces generated by the mask and tube. Subtracting ΔP_i from the appropriate metabolic rate (P_i) measured from the masked bat thus provides an estimate of the bat's power input (P'_i) during flight that is unhindered by the mask and tube force components which act along an axis parallel to the direction of air flow, or

$$P'_i = P_i - \Delta P_i.$$ (17)

Mask and air tube drag

Mask drag (D_m) was determined by measuring the change in drag force that resulted from placing the mask on a wingless bat model mounted on a flight balance. The *P. hastatus* model was a stuffed skin. The *P. gouldii* model was constructed from styrofoam, the ,dimensions and shape of which were determined from photographs of the flying bat and measurements made on the resting animal. The bat model was attached to a vertical brass rod ($0·15$ m long, $3·0 \times 10^{-3}$ m diam.) whose other end was attached to a one-component strain gauge flight balance contained inside a streamlined housing unit. The strain gauges of this flight balance formed a four arm bridge, and bridge imbalance was measured by integrating voltage over a period of 20 sec with a digital voltmeter. The flight balance was calibrated by attaching weights to a thread which ran over a pulley. They exerted a force on the flight balance/bat model system in the same direction as the drag forces. The flight balance gave a linear output over the range of drag forces encountered. The systematic error was negligible and the standard errors of drag force measurements made on this flight balance are $1·0 \times 10^{-3}$ N or less.
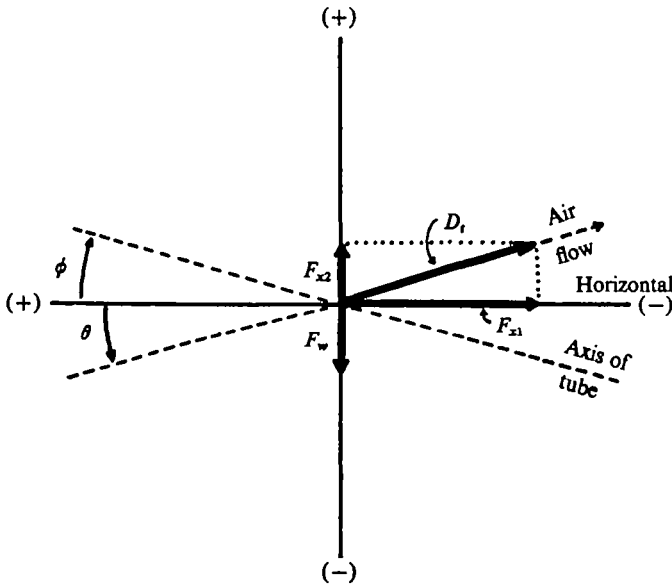
Fig. 4. Diagram showing various force components which relate to the quantification of the magnitude of the aerodynamic drag of the air tube that trailed behind the flying bat at angle ϕ from horizontal. See text for additional details.

The aerodynamic drag of the tubes (D_t) suspended in air by bat 2 and by *P. gouldii* was determined by measuring the angle (ϕ) relative to horizontal at which the tube trailed freely in the air from the mask to the floor of the tunnel. The angle ϕ was measured with a protractor at each combination of tunnel angle (θ) and air speed with a systematic error of less than 0·5° and an imprecision estimated to be 0·3°.

Assuming the tube generates a negligible lift-force, the angle ϕ is determined by the vector sum of two forces, aerodynamic drag and weight, acting along the tube's length (Fig. 4).

The tube's aerodynamic drag vector, which by definition acts along an axis parallel to and in the same direction as air flow, can be resolved into two components, F_{x_1} and F_{x_2}, acting along the horizontal and vertical axis respectively (Fig. 4). Thus,

$$\tan \theta = F_{x2}/F_{x1} \tag{18}$$

and
$$\tan \phi = (F_w + F_{x2})/F_{x1}, \tag{19}$$

where F_w is the weight vector of the length of the tube suspended in air by the flying bat. Combining equations (18) and (19), and solving for F_{x1} and F_{x2} yields

$$F_{x1} = F_w/\tan \phi - \tan \theta, \tag{20}$$

and
$$F_{x2} = F_{x1} \tan \theta. \tag{21}$$

The magnitude (D_t) of the tube's aerodynamic drag is then given by the relation

$$D_t = \sqrt{[(F_{x1})^2 + (F_{x2})^2]}. \tag{22}$$

D_t values for bat 2 and for *P. gouldii* were then substituted into equation (7) to calculate the total force (F_t) generated by the tubes of these two individuals.

A different method was used to determine the magnitude of F_t values for bat 1, since part of this individual's tube was supported by a ring stand. The total force component (F_t) generated by this bat's tube was measured directly at each combination of θ and V using the previously described one-component flight balance. The rod of this balance passed through a hole in the test section's ceiling to the point at which bat 1 was observed to fly at the particular set of tunnel conditions under consideration. The rod was oriented perpendicular to the direction of air flow. The drag of the rod was first measured and then subtracted from the force measured from the rod/tube system to obtain the additional force component bat 1 had to balance when flying with the air tube. F_t thus represents the total force component acting in the direction of air flow, and is the sum of the tube's aerodynamic drag (D_t) and the gravitational force component (F_{gt}) of the suspended tube acting along an axis parallel to the direction of air flow.

RESULTS

Drag of the masks and tubes

The aerodynamic drag of the masked model of *P. hastatus* was statistically indistinguishable at all air speeds from that of the unmasked model. Mask drag (D_m) has therefore been considered to be negligible for this species. For *P. gouldii*, mask drag $(D_m$, Newtons) increased with air speed $(V$, m s^{-1}) according to the linear least-squares relation

$$D_m = 0.00158V - 0.00664 \qquad (23)$$

(S.E. of estimate $= 0.00036$, $N = 5$).

For bat 2 and *P. gouldii*, the aerodynamic drag of the tubes (D_t) also increased in a linear manner with increasing air speed. The total force component (F_t) generated by the tube of bat 1 decreased in magnitude from 1.275×10^{-2} N at 6.2 m s^{-1} to 7.980×10^{-3} N at 9.0 m s^{-1} in the level tunnel. F_t values for bat 1 were inversely related to air speed because the long axis of the tube became oriented more parallel to the direction of air flow at higher air speeds as this individual maintained a flight position further downstream from the supporting ringstand.

Respiratory quotient

Each of the two individuals of *P. hastatus* had a mean respiratory quotient (R) for all flights of 0.93 (bat 1, S.D. $= 0.135$, $N = 12$; bat 2, S.D. $= 0.125$, $N = 24$), and that for *P. gouldii* was 0.88 (S.D. $= 0.070$, $N = 25$). These mean R values correspond to an energetic equivalent of oxygen of 2.075×10^7 J m^{-3} (4.96 kcal l^{-1}) for *P. hastatus*, and 2.050×10^7 J m^{-3} (4.90 kcal l^{-1}) for *P. gouldii*.

The respiratory quotient of each bat consistently decreased in value from one flight to the next on a given day (Table 1) even during a limited number of experiments where tunnel conditions were not altered from one flight to the next.

Partial efficiency

Partial efficiency values $(E_p$, equation 1) for the three bats varied with both speed and flight angle (Table 2). In the case of bat 1 there was no consistent relation between E_p and flight speed at a given θ, and E_p increased as θ became more

Table 1. *The relationship between flight number and mean respiratory quotient for the two species of bats investigated*

	Flight sequence* (±s.d., N)				
Species	1	2	3	4	5
P. hastatus (bats 1 and 2)	1·07 (±0·083, 8)	0·96 (±0·112, 8)	0·90 (±0·104, 7)	0·84 (±0·093, 7)	0·84 (±0·086, 5)
P. gouldii	0·94 (±0·034, 5)	0·92 (±0·064, 5)	0·90 (±0·077, 5)	0·85 (±0·063, 5)	0·82 (±0·037, 5)

* Each flight in a sequence of flights on a given day lasted approximately 15 min. The animals were allowed to rest approximately 5 min between flights. Flight conditions were varied randomly within a sequence and from one day to the next, except during a limited number of experiments.

Table 2. *Summary of partial efficiency values calculated for each of the three bats flying at various speeds and angles*

Species	Flight angles* used to compute ΔP_0	Flight angle(s) (θ) to which E_p value applies	Mean E_p† (range)
P. hastatus (bat 1)	+2° and 0°	+2	0·13 (0·12–0·15)
	+2° and −2°	0	0·19 (0·18–0·40)
	0° and −4°	−2°, −4°	0·34 (0·23–0·40)
P. hastatus (bat 2)	+2° and 0°	+2°	0·24 (0·19–0·29)
	+2° and −2°	0°	0·30 (0·24–0·40)
	0° and −4°	−2°, −4°	0·28 (0·23–0·33)
P. gouldii	0° and −2°	0	0·27 (0·22–0·31)
	0° and −4°	−2°, −4°	0·24 (0·22–0·27)

* See equation (2).
† Mean for all air speeds at indicated θ.

negative in value. E_p values for bat 2 tended to increase in magnitude at a given θ with increasing speed. For *P. gouldii*, E_p remained relatively constant at all flight conditions examined.

Uncorrected power input

The five P_i values measured (i.e. uncorrected for mask and tube forces) from a given bat at a particular flight condition were divided by body mass (m), and a mean P_i/m value (W/kg body mass) was calculated. The standard error of the mean for each of the various flight conditions examined was between 1·01 and 4·13 (mean s.e. = 2·56) for bat 1; 1·26 and 3·66 (mean s.e. = 2·42) for bat 2, and 0·36 and 1·30 (mean s.e. = 0·67) for *P. gouldii*.

Highest power inputs of bats during steady flight. I define the term $P_{i,h}/m$ for flying bats as the highest measured (i.e. uncorrected for mask and tube forces) power input per kilogram body mass obtained during flights lasting at least 12 min in duration. *P. hastatus* had a mean $P_{i,h}/m$ value of 130·4 W kg⁻¹ (s.d. = 2·82, N = 5), which was obtained from bat 2 during ascending flight (θ = +2°) at a speed of 8·95 m s⁻¹. Bat 1 was not capable of sustained flight at these tunnel conditions. *P. gouldii* yielded a mean $P_{i,h}/m$ value of 69·6 W kg⁻¹ (s.d. = 1·23, N = 5) during level flight at a speed of 9·86 m s⁻¹.
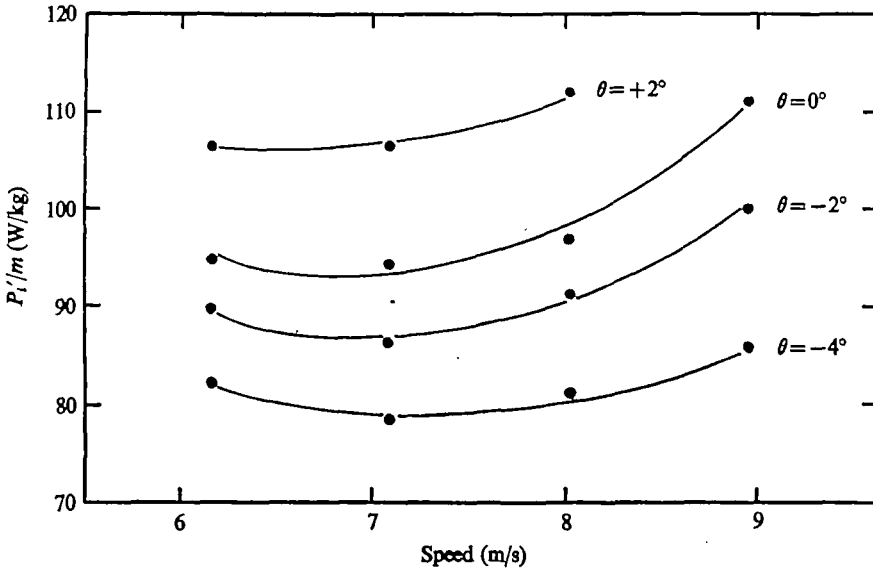
Fig. 5. Metabolic rate per unit body mass (P_i'/m) of *P. hastatus* as a function of air speed at various flight angles (θ). Each circle represents the mean of ten measurements (five from each *P. hastatus*) made at the indicated flight condition. The curved lines associated with these data represent the polynomial equations presented in Table 3.

Table 3. *Equations fitted by least squares to the relation between corrected power input* (P_i'/m, *W/kg*) *and air speed* (V, *m/s*) *at a given flight angle for* P. hastatus (*pooled data*)

Flight angle (θ)	Equation	S.E. of estimate [N]	Text equation number
+2°	$P_i'/m = 213\cdot34 - 33\cdot03V + 2\cdot54V^2$	4·246 [30]	(24)
0°	$P_i'/m = 311\cdot98 - 63\cdot08V + 4\cdot54V^2$	5·591 [40]	(25)
−2°	$P_i'/m = 274\cdot16 - 53\cdot13V + 3\cdot77V^2$	5·012 [40]	(26)
−4°	$P_i'/m = 213\cdot64 - 37\cdot02V + 2\cdot54V^2$	6·650 [40]	(27)

CORRECTED POWER INPUT

Power input data corrected for the influence of the mask and tube forces provide an estimate of an animal's power requirements during unencumbered flight. Corrections for mask and tube forces reduced the measured power input values obtained during level flight by 2–6% (bat 1), 9–12% (bat 2), and 10–15% (*P. gouldii*).

Corrected power input data (P_i'/m) from the two *P. hastatus* flying at the same wind-tunnel conditions showed close agreement with one another. The mean absolute deviation for all flight conditions examined was 4·8%, while that for level flight data only was 3·3%. Mean P_i'/m data for the two *P. hastatus* are illustrated in Fig. 5, and are described mathematically by the polynomial equations presented in Table 3. The lowest power input ($P_{i,l}'/m$) at a particular flight angle was at a speed of 7 m s^{-1} for all flight angles investigated. For level flight, *P. hastatus* had a mean $P_{i,l}'/m$ value of 94·2 W kg^{-1}. P_i'/m data for *P. gouldii* (Fig. 6, Table 4) showed the same general relation to air speed and flight angle as did that for *P. hastatus*. *P. gouldii* had a mean $P_{i,l}'/m$ value during level flight of 53·4 W kg^{-1} at a speed of 8 m s^{-1}.
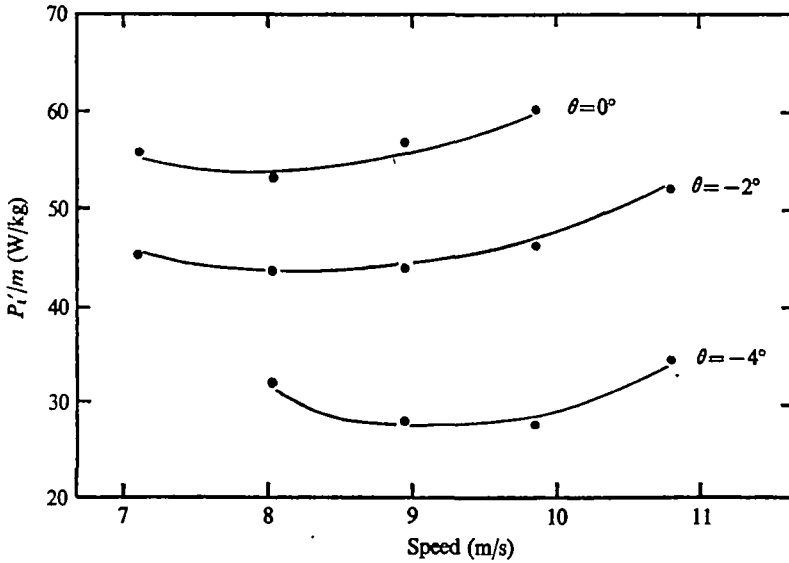
Fig. 6. Metabolic rates per unit body mass (P_i'/m) of *P. gouldii* at various combinations of air speed and flight angle (θ). Each circle represents the mean of five measurements made at the indicated flight condition. The curved lines associated with these data represent the polynomial equations presented in Table 4.

Table 4. *Equations fitted by least squares to the relation between corrected power input* (P_i'/m, *W/kg*) *and air speed* (V, *m s^{-1}*) *at a given flight angle for* P. gouldii

Flight angle (θ)	Equation	S.E. of estimate [N]	Text equation number
0°	$P_i'/m = 163 \cdot 25 - 27 \cdot 42V + 1 \cdot 72V^2$	1·716 [20]	(28)
−2°	$P_i'/m = 140 \cdot 15 - 23 \cdot 34V + 1 \cdot 41V^2$	1·338 [25]	(29)
−4°	$P_i'/m = 258 \cdot 61 - 49 \cdot 90V + 2 \cdot 70V^2$	1·258 [20]	(30)

DISCUSSION

Respiratory quotient. The mean values of R for the bats investigated in this study are comparable to those reported for both man and dogs during periods of moderate exercise lasting several minutes in duration. For example, Margaria, Edwards & Dill (1933) reported R values for exercising man that ranged between 0·8 and 1·0, depending on the intensity of work, during 10 min runs. The mean R values obtained in this study from flying bats are somewhat greater than those of flying birds. Tucker (1968, 1972) reported a mean R of 0·78 for the budgerigar (*Melopsittacus undulatus*) and 0·74 for the laughing gull (*Larus atricilla*) during flight.

It was mentioned previously that the respiratory quotient of each bat consistently decreased from one flight to the next on a given day (see Table 1). Man (Dill, Jones & Edwards, 1934; Dill, Edwards & de Meio, 1935) and dogs (Issekutz, Paul & Miller, 1967) also show a gradual reduction in R values with time during prolonged periods of moderate work.

Partial efficiency. E_p values obtained from *P. hastatus* and *P. gouldii* (Table 2) are similar to those reported for flying birds, despite the differences in wing
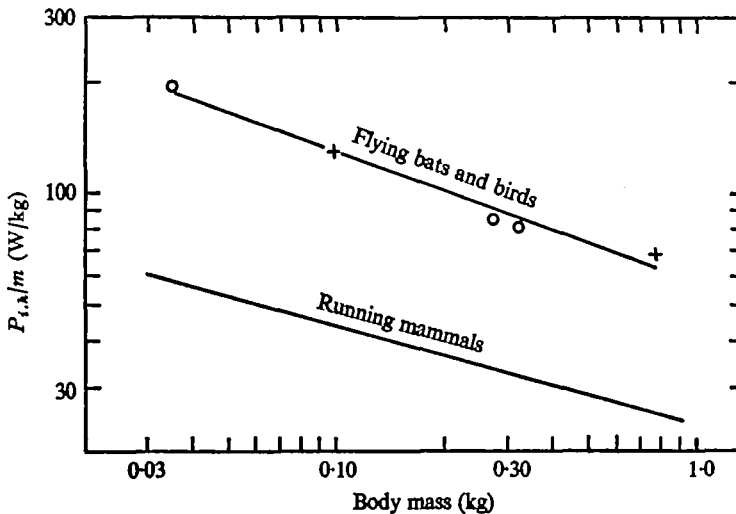
Fig. 7. Comparisons of the highest metabolic rates per unit body mass ($P_{i,\lambda}/m$) measured from flying bats (crosses) and birds (circles), and running mammals of various body masses. Mean $P_{i,\lambda}/m$ values shown for flying birds are (from left to right) the budgerigar, 198·6 W/kg (Tucker, personal communication); the fish crow, 85·7 W/kg (Bernstein *et al.* 1973: unpublished data); and the laughing gull, 81·7 W/kg (Tucker, personal communication). The line for flying vertebrates was fitted as described in text, and represents text equation (32). The line for running mammals represents equation (33) in text.

morphology found in these two groups. The budgerigar has E_p values which range from 0·19 to 0·28 during level flight at various speeds, and the laughing gull has a E_p value of 0·3 during flight at 11·7 m s^{-1} (Tucker, 1972). The fish crow (*Corvus ossifragus*) has E_p values between 0·22 and 0·38 during descending flight at various speeds (Bernstein, Thomas & Schmidt-Nielsen, 1973).

Partial efficiency values for both flying bats and birds are similar to those of some larger-size terrestrial mammals. Dogs have maximal E_p values that range from 0·18 to 0·29 in various individuals running at a speed of 1·62 m s^{-1} (Young *et al.* 1959), and man has E_p values between 0·20 and 0·35 (Margaria, 1938; Erickson *et al.* 1946). Some other terrestrial mammals (mice, chimpanzees), however, appear to be capable of E_p values that are more than twice as great as those for the above animals (Taylor, Caldwell & Rowntree, 1972).

UNCORRECTED POWER INPUTS

Highest power inputs of flying bats and birds, and exercising terrestrial mammals. Data obtained in this study show that the highest power inputs per unit body mass ($P_{i,\lambda}/m$, W/kg) of bats during steady flight are about the same as those predicted for flying birds of the same body mass, and considerably greater than those of running mammals. I define the term $P_{i,\lambda}/m$ for flying birds as the highest measured (i.e. uncorrected for mask and tube forces) power input per kilogram body mass obtained during flights lasting 5 min (the budgerigar) or longer (the fish crow and the laughing gull).

Pasquis *et al.* (1970) have measured what they consider to be maximal rates of

oxygen consumption ('max $\dot{V}_{O_2}$') from various smaller-size mammals running to exhaustion on a treadmill for periods lasting less than 2 min. In the case of running mammals, $P_{i,h}/m$ is equivalent to the term max $\dot{V}_{O_2}$ after the latter has been converted to the units of the present study.

$P_{i,h}/m$ data obtained from flying bats are compared with those available for flying birds and running mammals in Fig. 7. It can be seen that *P. hastatus* and *P. gouldii* both have metabolic capabilities comparable to those one would expect for flying birds of the same body mass. The least-squares equation fitted to these data from both flying bats and birds is

$$\log (P_{i,h}/m) = 1.765 - 0.35 \log m \tag{31}$$

(S.E. of estimate = 0.034, $N = 5$), or

$$P_{i,h}/m = 58.21 \ m^{-0.35}. \tag{32}$$

The mean absolute deviation of measured $P_{i,h}/m$ values for both bats and birds ($N = 5$) from those predicted from equation (32) is 5.5%, and the mean absolute deviation for bat data alone ($N = 2$) is 5.3%. The highest power inputs of small-size running mammals ($m = 0.030$ to 0.960 kg) also have a logarithmic relation to body mass (Pasquis *et al.* 1970):

$$P_{i,h}/m = 23.75 \ m^{-0.27}. \tag{33}$$

Thus, the ratio (R_1) of $P_{i,h}/m$ for flying bats and birds, and running mammals is given by the relation

$$R_1 = 2.45 \ m^{-0.08}. \tag{34}$$

R_1 has a value of 3.2 for animals with a mass of 0.035 kg, and 2.5 for animals with a mass of 0.780 kg.

It is worth while to note that the mean $P_{i,h}/m$ value reported for *P. hastatus* in the present study is 7% or 18% less than the mean metabolic rate obtained in a previous study from two tethered *P. hastatus* undertaking circular flight (Thomas & Suthers, 1972). However, since the tethered bats would usually only maintain these metabolic rates for approximately 3 min of flight, they do not qualify as $P_{i,h}/m$ values as defined in the present study.

CORRECTED POWER INPUTS

In the remainder of this paper, all power inputs for flying animals refer to values which have been corrected for the influence of mask and tube forces (i.e. P'_i/m, W/kg).

Comparison of power inputs for bats and birds. How do the power requirements of bats in level flight compare with those of birds? At a speed of 8 m s^{-1}, P'_i/m decreases with increasing body mass (Fig. 8). Both *P. hastatus* and the budgerigar show a rapid increase in P'_i/m above a particular air speed. This increase occurs at a lower air speed for *P. hastatus* than for the budgerigar. Even when *P. hastatus* flew in the level tunnel without the mask and air tube, the highest speed it would maintain (about 10 m s^{-1}) is still less than that of the masked budgerigar. *P. gouldii*
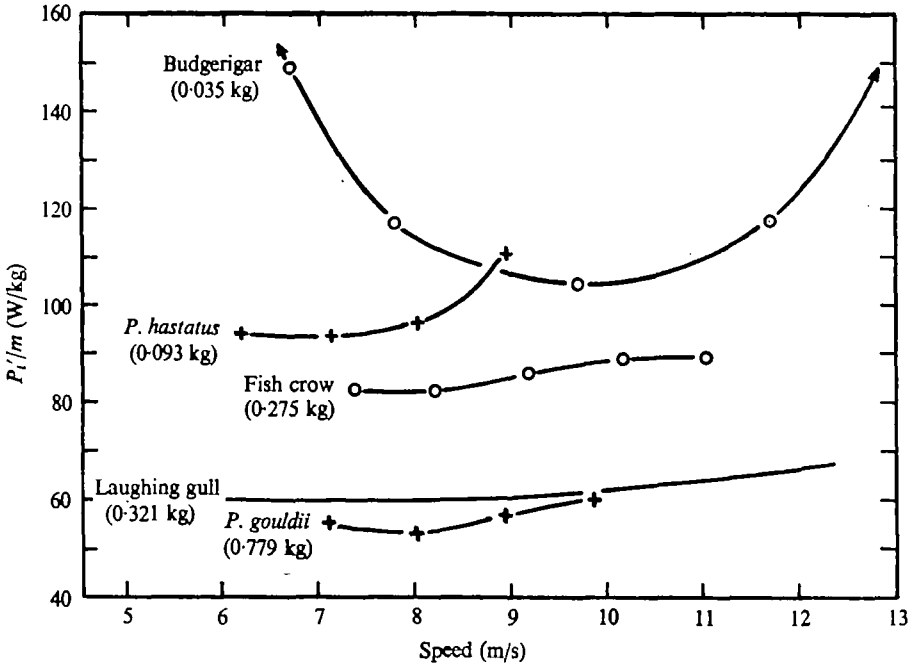
Fig. 8. Comparison of metabolic rates per unit body mass (P'_i/m) of bats and birds during level flight at the indicated air speeds. Data for the budgerigar and laughing gull were calculated from Tucker (1972; his table 1 and his equation (24) respectively). Data for the fish crow were calculated from Bernstein et al. (1973) and represent values predicted for level flight from metabolic data collected during descending flight. Data for bats are from Tables 3 and 4.

and the larger birds show relatively little variation in P'_i/m during level flight over the range of speeds for which data are available. During level flight, the laughing gull has a metabolic rate which is about one-third less than that of a similar-size fish crow (see Bernstein et al. 1973). P. gouldii has a body mass which is more than twice that of the laughing gull. Despite this difference in body mass, P'_i/m values for P. gouldii during level flight are only from 9% ($V = 8\cdot0$ m s^{-1}) to 3% ($V = 9\cdot9$ m s^{-1}) less than those of the laughing gull (Fig. 8).

Lowest power input during level flight. It is worth while to relate the lowest power inputs ($P'_{i,l}/m$) of P. hastatus and P. gouldii during level flight to those of birds, and compare these values with the highest power inputs predicted for running mammals. Data from bats and birds in level flight fall along a straight line when $P'_{i,l}/m$ is plotted on double logarithmic coordinates against body mass (Fig. 9). The ratio (R_2) of $P'_{i,l}/m$ for flying vertebrates (see legend, Fig. 9), and $P_{i,h}/m$ for running mammals (equation 33) can be calculated for animals of various masses. R_2 has a value which ranges from 1·9 ($m = 0\cdot035$ kg) to 2·2 ($m = 0\cdot780$). Thus, even the lowest P'_i/m values of bats and birds in level flight are about twice the highest predicted metabolic capabilities of similar-size terrestrial mammals.

Cost of transport. One objective of flight is to enable animals to move from one place to another, and it is of interest to compare the energetic cost of locomotion. Cost of transport (C) is the ratio of P'_i to the product of body weight (newtons)
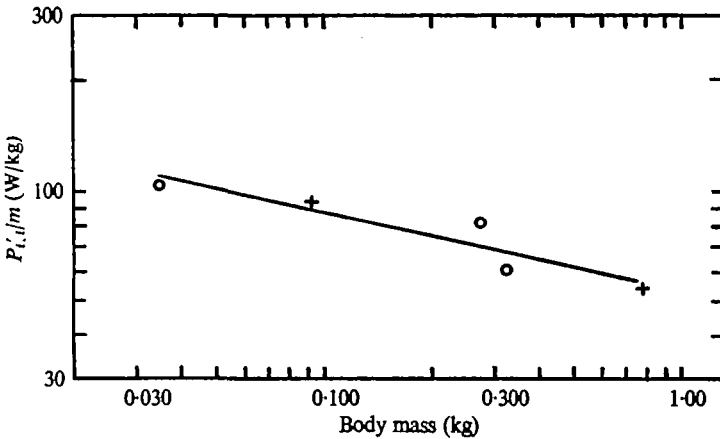
Fig. 9. The relationship between mean $P'_{i,l}/m$ and body mass for bats (crosses) and birds (circles) during level flight. The line associated with these data was fitted by the least squares method, and is given by the relation $\log (P'_{i,l}/m) = 1\cdot721 - 0\cdot223 \log m$ (s.e. of estimate $= 0\cdot056$, $N = 5$), or, $P'_{i,l}/m = 52\cdot54 \, m^{-0\cdot223}$. The mean absolute deviation of bird data ($N = 3$) from this line is $11\cdot6\%$, and that for bat data ($N = 2$) is $6\cdot0\%$. Values based on data from Fig. 8.
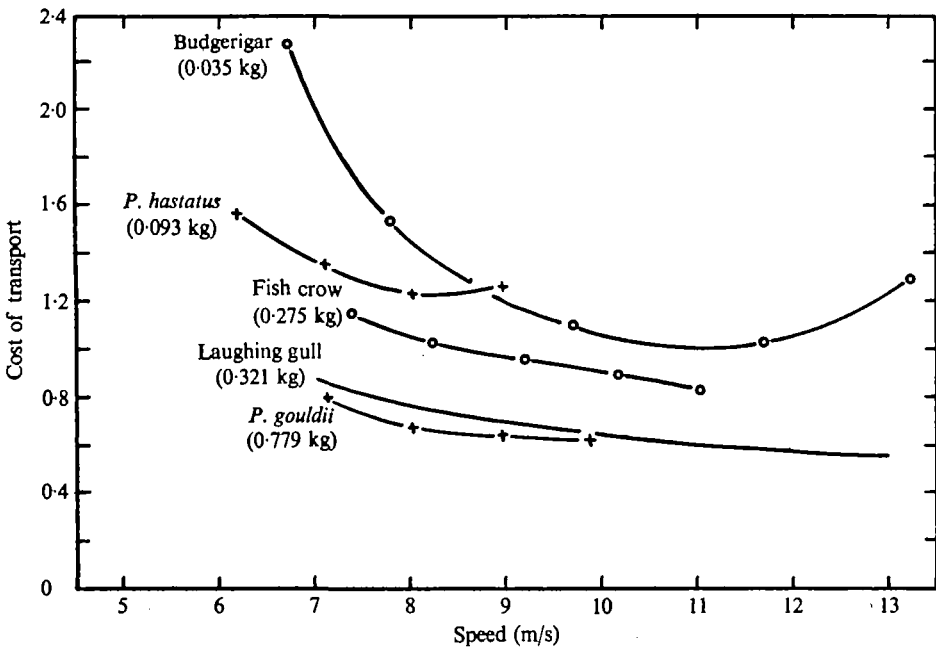

Fig. 10. Comparison of cost of transport values for bats and birds of various body masses during level flight over the indicated ranges of speed. Calculated from data in Fig. 8.

and speed (m s^{-1}). It is a dimensionless number such that the higher the value of C the greater the amount of energy an animal of a given weight must expend to travel a unit distance

Cost of transport data calculated for various bats and birds in level flight at various speeds are summarized in Fig. 10. *P. hastatus* has a minimum C value of $1\cdot23$ at
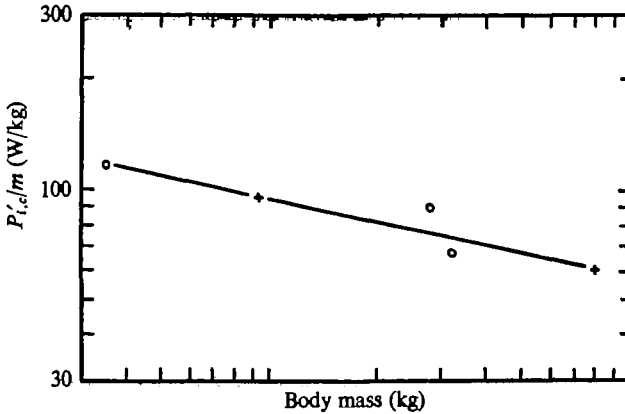
Fig. 11. The relationship between power input per unit body mass during level flight at the speed where cost of transport is minimum for each species ($P'_{i,c}/m$), and body mass. The line associated with these data from bats (crosses) and birds (circles) was fitted as described in text, and represents equation (36). Data from Figs. 8 and 10.

a flight speed of $8 \cdot 0$ m s^{-1}, which is close to the speed ($8 \cdot 3$ m s^{-1}) at which this bat has been reported to fly in nature (Williams, 1968). Cost of transport decreases with increasing flight speed in the three larger animals shown in Fig. 10. For *P. gouldii*, C has a minimum value of $0 \cdot 63$ during flight at a speed of $9 \cdot 9$ m s^{-1}.

Flying bats, like flying birds (Tucker, 1970), are capable of moving substantially greater distances per unit of energy consumed than walking or running mammals of equivalent size. Tucker has summarized minimum cost of transport data for various size walking and running mammals by an equation (equation (5); Tucker, 1970) which relates minimum C to body mass. Calculations based on this equation and minimum C values for bats indicate *P. hastatus* requires only one-sixth the energy to cover a given distance as does the same size terrestrial mammal, while *P. gouldii* requires one-fourth the energy of the same size terrestrial mammal.

Approximations of power inputs of bats and birds flying in nature. The power inputs of bats and birds in level flight may be compared at the flight speed where C is minimum for each species (i.e. P'_i/m at minimum C, $P'_{i,c}/m$). $P'_{i,c}/m$ has a consistent biological significance for each animal in that by flying at the speed where C is minimum, the animal can travel the greatest distance per unit energy consumed when there is no wind.

Some data are available indicating that at least certain species of bats and birds fly in nature at speeds comparable to those at which wind-tunnel studies show C is minimum for these species. As mentioned previously, the speed where C is minimum for *P. hastatus* flying in the wind-tunnel is only 4% less than the speed at which this bat has been reported to fly in nature. The speed at which the laughing gull has been reported to fly in nature ($12 \cdot 6$ m s^{-1}; Tucker & Schmidt-Koenig, 1971) is the same as that where C was minimum in wind-tunnel studies on this species (Fig. 10). Although I was unable to find reliable measurements of the speeds at which *P. gouldii* and the fish crow fly in nature, $P'_{i,c}/m$ values for these larger-size animals are not very sensitive to small changes in flight speed (see Fig. 8).

Presently available data from bats and birds in level flight fall along a straight

line when $P'_{i,c}/m$ is plotted on double logarithmic coordinates against body mass (Fig. 11). The least-squares equation fitted to these data is

$$\log(P'_{i,c}/m) = 1.77 - 0.214 \log m \tag{35}$$

(S.E. of estimate $= 0.047$, $N = 5$) or

$$P'_{i,c}/m = 58.4\ m^{-0.21}. \tag{36}$$

For reasons presented above, equation (36) provides the best available empirically derived means of approximating P'_i/m values from body mass data alone for bats and birds during horizontal flight in nature. The foregoing statement assumes, of course, that the bat or bird flies in nature at a speed where C is minimum in value for the species under consideration, and that there is no wind.

Comparisons of measured values, and theoretical predictions of power inputs for bats during level flight. Pennycuick (1969) has published a flight theory that enables one to predict the energetic cost of avian flight from a small number of easily measurable parameters. Tucker (1973) has added some new features to Pennycuick's theory, and has adjusted various parameters so that predictions made by this modified theory fit data measured from budgerigars and laughing gulls more closely. Tucker's modifications also improved the agreement between theoretical predictions and existing measurements from fish crows, and measurements from *P. hastatus* and *P. gouldii* in level flight at a speed of 8.0 m s^{-1} and 9.0 m s^{-1} respectively (see Tucker, 1973; his fig. 13 and his table 2).

In the following section I will examine how closely P'_i/m values obtained in this study from *P. hastatus* and *P. gouldii* during level flight at various speeds compare with theoretical power inputs calculated from Tucker's (1973) modified flight theory. While it must be emphasized that certain parameters of Tucker's theory have been adjusted so that predictions fit measurements from birds more closely, the same general aerodynamic principles and relationships presented in this theory also apply to bat flight.

The basal metabolic rate for each species of bat ($P_{i,B}$ in Tucker's equation 49) was estimated from an allometric equation derived from that presented by Brody (1945) which describes the relation between basal metabolic rate and body mass for placental mammals. Such calculations indicate a basal metabolic rate of 0.585 W for a 0.093 kg. *P. hastatus*, and a basal metabolic rate of 2.796 W for a 0.779 kg. *P. gouldii*. As mentioned previously, *P. hastatus* and *P. gouldii* have wing-spans (B in Tucker's equation 49) of about 0.45 m and 1.2 m respectively. The above values together with an appropriate air speed (V) were substituted into Tucker's (1973) equation (49), and theoretical power inputs were calculated. Dividing these values by the appropriate mean body mass provides theoretical estimates of P'_i/m values for each species during level flight.

These theoretical values are compared with actual mean P'_i/m values in Fig. 12. One can see that Tucker's modified theory underestimates P'_i/m values obtained from *P. hastatus* during level flight at all speeds. The deviations of the theoretical values from actual mean P'_i/m values calculated for *P. hastatus* from equation (25) in Table 3 range from 9.4% (when $V = 6.18$ m s^{-1}) to 24.4% (when $V = 8.95$ m s^{-1}). Tucker's modified theory overestimates actual mean P'_i/m values calculated for
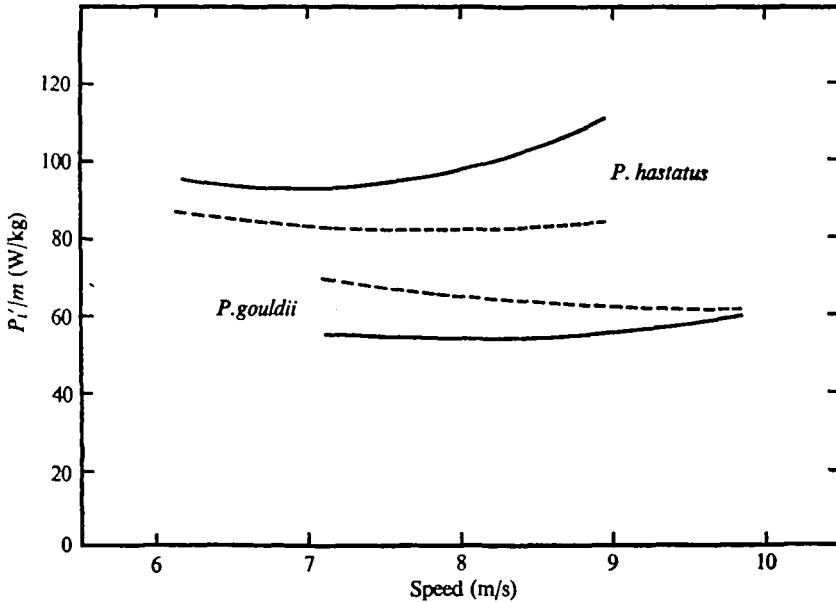
Fig. 12. Comparison of theoretical (broken curves) and actual (unbroken curves) P'_i/m values for *P. hastatus* and *P. gouldii* during level flight over the indicated range of speeds. The theoretical curves were calculated from Tucker's (1973) modified flight theory as described in text. Actual curves were calculated from text equations (25) (*P. hastatus*) and (28) (*P. gouldii*).

P. gouldii from equation (28) in Table 4 by from 24·1 % (when $V = 7\cdot11$ m s^{-1}) to 1·8 % (when $V = 9\cdot86$ m s^{-1}).

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