GAS EXCHANGE AND ENERGY COST OF FLIGHT IN THE WHITE-NECKED RAVEN, *CORVUS CRYPTOLEUCUS*

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SUMMARY

Energy expenditure during steady-state, wind tunnel flights was estimated from O_2 and CO_2 exchange in five white-necked ravens (*Corvus cryptoleucus*, mean mass, 0·48 kg) at air speeds of 8–11 m/s. Power input was closely similar to allometric predictions based on data from other species of smaller birds. It increased significantly with air speed and flight angle above horizontal, and decreased with increasing angles below horizontal. Maximum power input reached seven times the preflight value measured under resting but not basal conditions, 14 times the previously measured basal values and three times the calculated maximum for a similar sized running mammal. Energy cost to travel 1 km decreased with increasing air speed. These trends are similar to those previously observed in smaller birds.

INTRODUCTION

Recent studies utilizing wind tunnels have greatly increased the information available on the physiology of birds during forward flight. In birds, respiratory gas exchange has been well examined during flight under defined aerodynamic conditions. Data have been obtained for several species spanning a 10-fold range of body mass, from 0·03 to 0·3 kg and have been utilized to calculate metabolic rate during the steady state (Tucker, 1968, 1972; Bernstein, Thomas & Schmidt-Nielsen, 1973; Butler, West & Jones, 1977; Torre-Bueno & Larochelle, 1978). However, data have not been obtained for birds larger than 0·3 kg, except for transitory metabolic rates measured in the black duck (1·03 kg) for flights of less than 15 s duration (Berger, Hart & Roy, 1971).

To extend the range of body mass for which we have information we have studied gas exchange and energy use during steady-state, forward flight in the 0·48 kg white-necked raven (*Corvus cryptoleucus*), and have compared the data with those from other species.

Animals

The white-necked raven is a medium sized member of the family Corvidae occupying arid regions of the southwestern United States and Mexico (Mishaga, 1978). Seven ravens were captured as fledglings in southern New Mexico. The birds were maintained in captivity for 2–3 years on a diet of beef liver, pigeon and rat carcasses, a vitamin supplement, and water *ad libitum*, and were housed together in an outdoor aviary approximately 4 m wide × 8 m long × 3 m in height. All grew normally to adult size and remained in good health throughout this study.

Flight training

The ravens were trained to fly in a wind tunnel of open circuit design similar to that described by Tucker & Parrott (1970). Both upstream and downstream ends of the Plexiglas test section (1·5 × 1·5 × 3·5 m) were fitted with hardware cloth (1·27 cm mesh). Wind speed (V) could be varied from 8–11 m/s, while turbulence, determined as described by Tucker (1972), remained below 7 %. The tunnel could be tilted about the transverse axis at the rear of its test section, so that the tunnel's front end projected above or below horizontal. Since air flowed from front to rear, parallel to the test section floor, a bird flying forward followed an ascending, descending, or horizontal flight path, depending on the tilt of the tunnel. The training procedure utilized a collapsible perch mounted in the wind tunnel test section as described by Tucker (1968), but without the use of negative reinforcement in the form of electric shock. Daily training sessions lasted 30–60 min for each bird.

After the birds had learned to fly continually in the horizontal tunnel, they were trained to wear an individually fitted, cone-shaped mask constructed of transparent acetate. The mask covered the head but was open at the back in a manner similar to that described by Tucker (1972). A flexible vinyl tube (3·0 mm o.d.), trailing from the front of the mask during flight, drew air continuously from the mask for analysis of respiratory gases (see below). Preliminary experiments showed that the mask air flow, 11 l/min, was great enough to preclude any loss of expirate from the mask's rear margin. By the end of the 4–6 week training period, five birds (mean mass, 0·48 kg) would consistently fly wearing the mask and trailing the air tube during horizontal flights of 25–30 min maximum duration.

The aerodynamic drag of the mask and its trailing tube were measured at each flight angle (θ) using techniques described by Tucker (1972) and Bernstein *et al.* (1973). An additional downward increment of tilt, amounting to 0·2 ° or less, was calculated from the drag data and added to the wind tunnel angle, resulting in an actual flight angle of θ'. This imparted a gravitational component to thrust exactly equal and opposite to the drag of the mask and tube, and the effect of this drag on metabolic cost of flight was thus cancelled (Tucker, 1972). The flight angle increment is excluded from values reported herein, and the data presented thus correspond to the indicated θ.

Gas exchange measurements

Respiratory gas exchange was measured using a flow-through respirometry syst█

onnected through the air tube to the mask, as described previously (Hudson & Bernstein, 1981). Mask excurrent air was directed through a system of flow and pressure regulators, then through a dewpoint hygrometer, an infrared CO_2 analyser, and a paramagnetic O_2 analyser. These were connected to potentiometric chart recorders calibrated to provide information about the partial pressures of water vapour, of CO_2 and of O_2, respectively, in the mask excurrent air. This information, together with temperature, pressure, and flow rate of mask air, were utilized to calculate evaporative water loss, CO_2 production ($\dot{M}CO_2$) and O_2 consumption ($\dot{M}O_2$). The evaporative water loss data have been reported previously (Hudson & Bernstein, 1981).

Hereinafter, flight angles above horizontal will be indicated as positive, and those below horizontal as negative. Steady state measurements were made during flights of 10–30 min duration at air speeds from 8–11 m/s and flight angles, θ, from +2·5° to −4° (Table 1). Ambient temperature (T_a) during each flight was stable, and ranged from 18–32 °C. Resting rates of gas exchange were determined on the birds before and after each flight using the same system, except that the birds stood still on the perch or on the floor of the tunnel for 10–20 min. Resting $\dot{M}O_2$ was calculated from the lowest constant O_2 recording over this period. The body mass of each bird was measured to the nearest g after each series of flights.

For both resting and flying ravens, respiratory exchange ratio (R) was calculated as $\dot{M}CO_2/\dot{M}O_2$. An energy equivalent for O_2 was calculated for R during each $\dot{M}O_2$ measurement (Lusk, 1924), and metabolic rates were estimated therefrom. We assumed that all energy was derived from a mixed fat-carbohydrate source and that protein catabolism was insignificant.

RESULTS

As shown in Table 1, $\dot{M}O_2$ increased with V and θ, ranging from 6·4 mmol $O_2/$ (kg · min) at $V = 8$ m/s and $\theta = -4°$ to 10·3 mmol $O_2/($kg · min$)$ at $V = 10$ m/s and $\theta = +2·5°$. The minimum value for horizontal flight was 7·9 mmol $O_2/($kg · min$)$ at 8 m/s, and the highest value was 9·2 mmol $O_2/($kg · min$)$ at $V = 11$ m/s. We observed no variation in $\dot{M}O_2$ or $\dot{M}CO_2$ with T_a from 18–32 °C. The mean preflight $\dot{M}O_2$ was 1·58 mmol $O_2/($kg · min$)$ (s.d. = 0·24; $n = 5$).

The overall mean R, computed from the average for each bird under each set of flight conditions ($n = 73$) was 0·77 (s.d. = 0·05) (Table 1). The mean R for a particular set of flight conditions ranged from 0·73 at $V = 8$ m/s and $\theta = -4°$ to 0·85 at $V = 10$ m/s and $\theta = +2·5°$. The mean preflight R was 0·80 (s.d. = 0·09). R decreased with flight number on any given day. The mean decrease in R, 0·06 (s.d. = 0·05), from the first to the second flight of the day was significant ($P = <0·01$; paired t test) in 40 comparisons for which we had data under identical flight conditions. The data did not permit monitoring of changes in R during individual flights.

DISCUSSION

Respiratory exchange

The data on respiratory exchange ratios (Table 1) are in general agreement with eady state values reported for other birds during flight. Published R values range

Table 1. *The effect of speed and flight angle on oxygen consumption and respiratory exchange ratio* (R) *during steady state flight in the white-necked raven*

Values shown are means (s.e., *n*) of repeated measurements on up to five birds[1]. *n* values for *R* are the same as for corresponding oxygen consumption data.

Air speed (m/s)	Flight angle (degrees from horizontal)				
	−4	−2	0	+1	+2·5
	Oxygen consumption mmoles O_2/(kg · min)				
8	6·4 (0·2, 4)	6·5 (0·5, 5)	7·9 (0·3, 5)	8·2 (0·3, 4)	—
9	6·8 (0·3, 5)	7·4 (0·8, 5)	8·3 (0·4, 5)	9·0 (0·4, 3)	—
10	6·9 (0·7, 5)	7·6 (0·6, 4)	8·6 (0·3, 5)	9·2 (0·3, 4)	10·3 (0·2, 3)
11	7·4 (0·6, 4)	7·7 (0·8, 5)	9·2 (0·6, 4)	10·0 (0·8, 4)	—
	Respiratory exchange ratio				
8	0·73 (0·02)	0·73 (0·01)	0·75 (0·02)	0·73 (0·02)	—
9	0·77 (0·05)	0·76 (0·04)	0·76 (0·06)	0·74 (0·04)	—
10	0·76 (0·03)	0·77 (0·02)	0·82 (0·01)	0·82 (0·04)	0·85 (0·09)
11	0·78 (0·05)	0·78 (0·04)	0·77 (0·04)	0·78 (0·08)	—

[1] The response of a particular bird to one combination of speed and flight angle was determined as the mean of *N* individual flights, where *N* varied from 2–7, inclusive. The total number of individual flights was 266, for which the mean of all standard deviations was ± 4·0 %. The values presented in this table for each set of flight conditions are the means of *n* mean values for each bird.

from 0·69–0·78 (Tucker, 1968, 1972; Torre-Bueno, 1978; Torre-Bueno & Larochelle, 1978) except for a value of 0·93 for pigeons (Butler *et al.* 1977). Values reported for exercising mammals, including flying bats, range higher, from 0·8–1·0 (Thomas, 1975).

The low avian *R* suggests that fat is the major metabolic substrate used during flight. This statement rests on the assumption that the *R* during flight is a direct reflection of the metabolic respiratory quotient (*RQ*). However, it has long been known that *R* during exercise may also have acid-base and ventilatory components (Hill, Long & Lupton, 1924). For example, if the anaerobic threshold is exceeded, increases in lactic acid production will result in an increase in *R* above the metabolic *RQ* as a consequence of excess CO_2 elimination associated with bicarbonate buffering. Such changes tend to be transient, since *R* will not remain elevated above *RQ* once the CO_2 stores, lactate production and $\dot{M}O_2$ reach a steady state (Wasserman, van Kassel & Burton, 1967; Wasserman, Whipp, Koyal & Beaver, 1973). At that point, muscular anaerobic energy expenditure should appear as a component of whole-body, aerobic metabolic rate. Thus the interpretation of *R* in terms of the metabolic substrate utilized should not be affected as long as steady state values of $\dot{M}O_2$ and $\dot{M}CO_2$ are attained.

Deviation in *R* from *RQ* could also result from excess excretion of CO_2, as a consequence of the hyperpnoea associated with respiratory evaporative cooling during exercise at elevated ambient temperature. Indeed, respiratory ventilation increases 3-fold over the same range of T_a as used here (Hudson & Bernstein, 1981). However, the lack of correlation between T_A and $\dot{M}O_2$, $\dot{M}CO_2$, or *R* in this study suggests that significant parabronchial hyperventilation in excess of metabolic requirements m

ıt occur, at least during steady-state flight. It remains possible, however, that decreases in total CO_2 sustained before establishment of steady-state may create a hypocapnia maintained during the balance of the flight.

R has been reported to decrease with time during prolonged periods of moderate exercise in both mammals (Issekutz, Paul & Miller, 1967; Thomas, 1975) and birds (Tucker, 1968, 1972; Butler *et al.* 1977). We found significant reduction in R between first and second flight trials for a bird on a given day. This may reflect the depletion of carbohydrate stores and a change to increased dependence on fat during subsequent flights.

Power input

Effects of speed

We estimated specific power input for flight ($P_{i/m}$, W/kg) as metabolic rate, calculated from $\dot{M}O_2$ and the energy equivalent of O_2 for a particular R, divided by body mass. $P_{i/m}$ showed linear increases with speed over the range of V used (Fig. 1). The coefficients of the linear least squares regression equations were all significant (Table 2); however, the residual variance was excessive at $\theta = -2$ and $-4°$, as indicated by a low coefficient of determination (r^2). $P_{i/m}$ for horizontal flight ranged from 58·1 W/kg at 8 m/s to 68·4 W/kg at 11 m/s, while the highest mean recorded was 78·2 W/kg (s.d. = 1·2) at $\theta = 2·5°$ and $V = 10$ m/s.

The 18 % increase with speed in $P_{i/m}$ recorded for level flight in the raven is higher than the 8 % increase calculated for the fish crow, *Corvus ossifragus*, (Bernstein *et al.* 1973) over the same speed range. The data for the laughing gull, *Larus atricilla*,
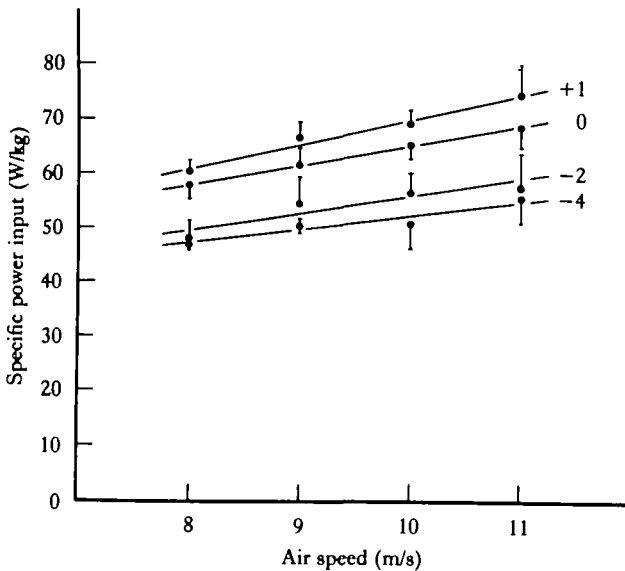

Fig. 1. Specific power input for flight ($P_{i/m}$) in relation to air speed (V) at different flight angles (θ). θ is indicated by numerals near each line. Points indicate the means of repeated measures on five ravens; vertical bars span 2 s.e. above or below these means. Solid lines are linear least-squares regression lines fitted to the data. Coefficients and statistics for the lines are given in Table 2.

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Table 2. *Linear regression analyses of the relation (Equation 1) between specific power input for flight* $(P_i/m)^1$ *and air speed* (V), *and of the relation (Equation 2) between power input* (P_i) *and the change in power output* $(\Delta P_o)^1$ *associated with flight at different angles* (θ)

	a	b	$s_{y \cdot x}$	s_b	r^2	F	n
			Statistical parameters				
Flight angle, (°)			Equation 1: $P_{i/m} = a + bV$				
+1	24·8	4·5	3·4	0·8	0·72	33·4	15
0	29·4	3·6	3·0	0·7	0·66	28·5	17
−2	24·7	3·0	5·5	1·4	0·30	7·0	18
−4	27·7	2·5	3·9	0·7	0·34	8·0	18
Air speed (m/s)			Equation 2: $P_i = a + b\Delta P_o$				
8	27·2	3·1	1·5	0·5	0·78	39·5	13
9	29·9	2·5	2·3	0·7	0·58	12·1	12
10	31·5	2·8	1·4	0·3	0·87	90·9	16
11	32·9	3·0	2·6	0·7	0·68	21·0	12

Abbreviations: a, constant; b, regression coefficient, $s_{y \cdot x}$, standard error of estimate; s_b, standard error of regression coefficient; r^2, coefficient of determination; F, variance ratio; n, total degrees of freedom.
[1] ΔP_o calculated as $WV(\sin \theta - \sin 0°)$, the maximum change in aerodynamic power requirements at any flight angle relative to horizontal.

(Tucker, 1972) and the starling, *Sturnus vulgaris*, (Torre-Bueno & Larochelle, 1978) show an even flatter relationship of $P_{i/m}$ to V over the same range of velocities. By way of contrast, it is interesting that aerodynamic and kinematic data for the rook, *Corvus frugilegus*, (Oehme, Oathe & Kitzler, 1977) indicate a steep rise in mechanical power output requirements (P_o) at these speeds. P_o increased 36 % between 8 and 11 m/s in the rook, similar in mass and morphology to white-necked ravens. If power input in the rook had increased in a manner similar to that in the raven, then the efficiency of flight, the ratio of power output to power input, would have doubled over the range from 8–11 m/s. Determining whether this actually occurs must await direct measurements of P_i in rooks.

The speed at which P_i for level flight was minimum in the ravens, 8 m/s, is similar to that in the laughing gull (Tucker, 1972), the fish crow (Bernstein *et al.* 1973), and the flying fox, *Pteropus gouldii* (Thomas, 1975). The speed of minimum power output calculated for the rook (Oehme *et al.* 1977) was 7 m/s. The predicted $P_{i/m}$ for horizontal flight at minimum power speed, from the equation of Thomas (1975), was 7 % above our value of 58·1 W/kg at $V = 8$ m/s. Furthermore, it must be considered that our value may overestimate the true minimum speed and $P_{i/m}$, since we could not test the ravens at speeds lower than 8 m/s.

We calculated the highest power input $(P_{i,h/m})$ from the maximum steady state MO_2 recorded from each bird. $P_{i,h/m}$ was 84·5 W/kg, seven times the preflight metabolism and over 14 times the standard metabolic rate reported by Lasiewski & Dawson (1967). Further, the measured $P_{i,h/m}$ was 12 % above the value predicted from Thomas's (1975) allometric equation for flying birds and mammals, and almost three times the value predicted for small running mammals by the equation of Pasqu
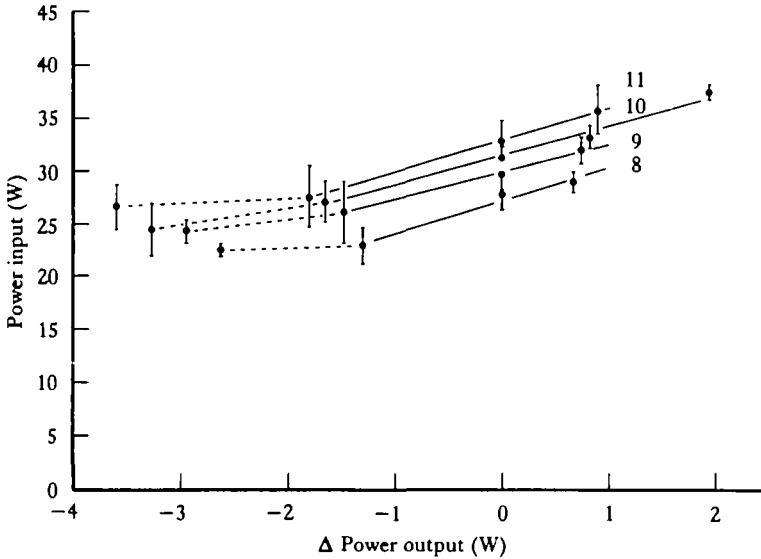
Fig. 2. Metabolic power input for flight (P_i) in relation to the theoretical increment in aerodynamic power output (ΔP_o) necessary to fly at a given flight angle (θ) with respect to horizontal flight ($\theta = 0$). ΔP_o is calculated as $WV(\sin \theta - \sin 0°)$, where W is weight in newtons. ΔP_o thus expresses the magnitude and direction of the change in power output required to fly at θ above or below the horizontal. Points indicate the means of repeated measurements on five ravens; vertical bars span 2 s.e. above and below the means. Solid lines are least-squares regression lines fitted over the linear range of the data. The numerals near each line indicate the air speed (m/s) at which the measurements were made. The dashed lines join means at the lower workloads where the relationships depart from linearity. Coefficients and statistics for the regression lines are given in Table 2.

Lacaisse & Dejours (1970). We could not determine whether the ravens could have achieved even higher rates of aerobic metabolism, because the air speed in the wind tunnel could not be increased beyond 11 m/s.

Effects of flight angle

P_i/m also increased with θ (Fig. 1). Since we wished to analyse the relationship of power expenditure to θ more directly, we replotted the data to show the relationship of P_i to ΔP_o (Fig. 2). The latter is the increment in power output associated with a change in flight angle from $\theta = 0°$ to another specified θ. ΔP_o is calculated as WV ($\sin \theta - \sin 0°$) $= WV \sin \theta$, where W is weight in newtons (Tucker, 1972; Bernstein *et al*. 1973; Thomas, 1975). The calculation assumes that the primary effect of an altered flight angle is a change in the contribution of body weight to thrust or drag forces.

The increase in P_i with ΔP_o was nonlinear over the range of θ employed (Fig. 2). Most of the nonlinearity occurred at the lowest θ, $-4°$; therefore we approximated the relationship with least-squares, linear regressions above this flight angle (Fig. 2). The equations were statistically significant ($P < 0.01$) at all speeds (Table 2). While the slopes were significantly different from zero, none was statistically distinguishable from the mean slope of 2·86 (s.e. = 0·22).

■Much of the nonlinearity in the curves of P_i vs ΔP_o may be due to experimental

design. The ravens often attempted to maintain position in the test section by gliding especially at $-4°$. This was deliberately discouraged, and the birds were therefore probably forced to expend more energy than they might have, if allowed to fly unperturbed. There was less tendency toward intermittent gliding at the higher work loads, where the P_i relationship was essentially linear (Fig. 2). Thus our full data set gives an estimate of the P_i for flapping flight at these angles, but does not contribute to our knowledge of the minimum power required to maintain position in the test section under all flight conditions. Tucker's (1968) $\dot{M}O_2$ data for budgerigars also showed marked curvilinearity with flight angle, and thus in ΔP_o, over the same range of speeds used in this study, as do the data of Bernstein et al. (1973) for fish crows. Nonlinear relationships between energy expenditure and work rate have been reported for walking (Donovan & Brooks, 1977) and cycling (Gaesser & Brooks, 1975) in humans as well.

Cost of transport

The measure of effectiveness of transporting a unit of body weight a unit of distance is the ratio of P_i to the product of the body weight and speed, P_i/WV (Tucker, 1970). The resulting value, referred to as the cost of transport (C), is a dimensionless number related to the efficiency of the transport process (Gabrielli & von Karman, 1950). A specific cost of transport (C') can be calculated as P_i/mV, expressed in units of specific energy per unit distance travelled (Table 3).

C' decreased with speed and with increasing size of the angle θ below horizontal. The minimum cost to travel 1 km during horizontal flight was $6·2 J/(g·km)$ at $V = 11 m/s$. This value falls almost exactly on the regression line relating log C' to body mass, calculated for flying animals ranging in size from a fruit fly to a pigeon (Tucker, 1970). The minimum C' for the ravens is also within $0·5 \%$ of the value calculated from Thomas's (1975) allometric equation relating $P_{i/m}$ at the speed of minimum C to body mass for several bird and bat species in wind tunnel flight. The speed at which C' was minimum, $11 m/s$, is within the range of $10–12 m/s$ reported for birds flying in wind tunnels (Tucker, 1968, 1972; Bernstein et al. 1973).

Efficiency

According to Tucker (1972, 1973), a partial efficiency (E_p) for work done by the

Table 3. *Specific cost of transport, defined in the text as* $C' = P_i/mV$, *at various combinations of air speed and flight angle, where* P_i *is power input, m is body mass, and V is flight speed*

Values calculated from data presented in Fig. 1 and expressed as means (2 s.e.). Units are J/(g·km).

| | Flight angle (degrees from horizontal) | | | | |
Air speed (m/s)	−4	−2	0	+1	+2·5
8	5·9 (0·2)	6·0 (0·5)	7·3 (0·4)	7·6 (0·3)	—
9	5·6 (0·1)	6·1 (0·7)	6·9 (0·3)	7·4 (0·3)	—
10	5·1 (0·5)	5·7 (0·4)	6·5 (0·2)	6·9 (0·2)	7·8 (0·1)
11	5·0 (0·4)	5·2 (0·6)	6·2 (0·4)	6·8 (0·5)	—

▌rust of a bird's wings can be calculated as the ratio of the change in P_o to the change in P_i between any two flight angles. Alternatively, E_p can be estimated using linear regression when P_i is plotted as a function of the change in P_o, as in Fig. 2. E_p then equals the reciprocal of the slope at any given air speed (Pennycuick, 1975).

The mean E_p for the ravens, as calculated by the latter method, was 0·35 (range, 0·32–0·40) for all flight speeds over the linear part of the curves in Fig. 2. The results are summarized in Table 2. Tucker (1972) reported an E_p of 0·3 for the laughing gull, whereas Bernstein *et al*. (1973) estimated a mean value of 0·25 for the fish crow (range 0·22–0·29). E_p for the budgerigar ranged from 0·18–0·29 (Tucker, 1968), while Thomas (1975) reported a range of 0·13–0·34 for two bat species. E_p for the raven is thus at the upper end of the range of E_p reported previously for flying birds and bats.

It is not apparent why E_p estimates should be higher for the raven than values reported for other species flying under purportedly similar conditions. It may be, as Tucker (1968) originally suggested, that the parasite drag coefficient actually decreases with increasing θ relative to horizontal, due to possible changes in body attitude. If this is true $WV \sin \theta$ will overestimate the actual change in power output, which would result in an inflated estimate of efficiency. Changes in body attitude with flight speed may be partially responsible for the lower than predicted change in power expenditure with speed in the starling (Torre-Bueno & Larochelle, 1978), but we have no measurements to indicate if there is a corresponding change with flight angle in ravens.

It is common to compare physiological measurements of P_i as a function of flight speed with estimates of mechanical power output, calculated from various applications of aerodynamic theory or kinematic methodology (e.g. Tucker, 1973). Such comparisons require knowledge either of the whole animal's efficiency in converting metabolic fuel to aerodynamic work (Pennycuick, 1975), or of the *in vivo* flight muscle efficiency coupled with the fraction of P_i not directly involved in external work production (Tucker, 1973). Unfortunately, methods of estimating efficiency which rely on incremental changes in work load, such as those used in this study, measure neither muscle efficiency nor the total efficiency during exercise (Stainsby, Gladden, Barclay & Wilson, 1980). Furthermore, muscle efficiency may depend upon flight speed in an, as yet, unpredictable way (Rayner, 1979). Since there are no accurate values yet available for the above parameters, we make no attempt to equate our physiological P_i measurements to predictions of flight power requirements based upon theoretical or empirical aerodynamic models for bird flight. We heartily concur with Oehme *et al*. (1977) that efficiency estimates, obtained under precisely defined conditions, using both physiological and kinematic techniques to determine power relationships simultaneously, are sorely needed.

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