Metabolism during flight in the laughing gull, *Larus atricilla*

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WILD BIRDS PERFORM prodigious feats of exercise by human standards. For example, ducks can fly at speeds in excess of 17 m/sec (25), probably for hours, and small birds migrating over deserts and oceans are thought to fly nonstop and without feeding for distances exceeding 1,000 km and times exceeding 50 hr (8, 14, 15). Some birds appear to be more tolerant of high altitudes than any other vertebrates, as they have been seen in flapping flight at altitudes in excess of 6,000 m (21). What are the metabolic rates of the birds during such feats?

The metabolic rate in flight is a function of both the speed and the angle of flight, and these variables can be controlled if a bird is trained to fly in a wind tunnel. Metabolic rates during flight in a wind tunnel at controlled speeds and angles are available for two animals, the budgerigar (*Melopsittacus undulatus*) (22) and the laughing gull (*Larus atricilla*). (23)

In an ideal wind tunnel, the behavior of a stationary object exposed to moving air in the test section is identical to the behavior of the object moving through stationary air. Actual wind tunnels are not ideal, and in addition, a bird flying in one can be attached to instrumentation which its wild counterpart is not. In this study I will quantify some of the differences that occur between the metabolic rate of a gull flying in a wind tunnel and one flying in still air in nature.

The description of the aerodynamic forces on an object in free flight in a wind tunnel can be complicated, for, with
the exception of gliding or diving, flight requires that some parts of the object move relative to other parts. Thus, the vectors \( V \), lift, and drag all will have different values for different parts of the object; and, for a given part, all will vary with time. For example, in flapping flight, \( V \), lift, and drag at any instant vary from the wing tip to the wing base; and at any one wing region, they vary throughout the stroke cycle (see ref. 3 for a detailed discussion).

On the average, over a stroke cycle, bird wings produce a mean aerodynamic force that can be resolved into a lift component (\( L \)) and a drag component (\( D \)), where the directions of the components are defined by the direction of \( V \) relative to coordinates originating on the bird’s body exclusive of the wings. The drag component is negative in sign and is commonly called thrust (\( T \)). Thus, for a bird flying in a wind tunnel in which \( V \) is inclined to horizontal by angle \( \theta \):

\[
L = -W \cos \theta
\]

and

\[
T = -(D + W \sin \theta)
\]

where \( D \) is the drag of the bird's body exclusive of the wings and \( \theta \) is positive when \( V \) has a downward component (Fig. 1). For the remainder of this paper, the symbols \( V \), \( L \), \( D \), and \( T \) when applied to birds will be used strictly with the meanings that they have in the first sentence of this paragraph and in equations 1 and 2.

By tilting the longitudinal axis of a wind tunnel in which a bird is flying, one can quantitatively add to or subtract from the magnitude of \( T \) without changing the magnitude of \( L \) appreciably. When the tunnel is tilted through angle \( \theta \) so that the air velocity vector has an upward component (\( \theta \) negative), the aerodynamic and gravitational forces on the bird are exactly the same as if the bird flew downward in still air along a path inclined at \( \theta \) to horizontal. Ascending flight is duplicated if the tunnel is tilted to positive values of \( \theta \).

The aerodynamic forces acting on an object under specific conditions can be used to predict the aerodynamic forces under other conditions if the Reynolds number for the specific conditions is known. Reynolds number is non-dimensional and is defined as:

\[
Re = \frac{\rho V d}{\mu}
\]

where \( \rho \) is air density (1.18 kg/m\(^3\) in this study), \( V \) is the air velocity relative to the object, \( d \) is some specified linear dimension of the object, and \( \mu \) is the dynamic viscosity of air. The ratio \( \rho/\mu \) in this study has the value 65,200.

Lift and drag forces on an object are often described in terms of nondimensional lift and drag coefficients (\( C_L \) and \( C_D \), respectively) because these coefficients are functionally related to \( Re \) and are almost constant over certain ranges of \( Re \) values. Thus:

\[
C_L = \frac{2L}{\rho S V^2}
\]

and

\[
C_D = \frac{2D}{\rho S V^n}
\]

where \( S \) is some specified surface area of the object.

METHODS

Experimental Animals

The two gulls used in this study were hand reared from chicks and kept in an outdoor cage 6.1 m wide, 6.1 m long, and 3.7 m high. They were fed on raw fish and canned cat food. Their masses varied between 0.26 and 0.36 kg unless otherwise noted.

The gulls were trained to fly freely in an open-circuit wind tunnel that was mounted on a cradle so that its long axis could be tilted up to 8° from horizontal. The wind tunnel and the characteristics of the airflow in the test section are described in detail in the study of Tucker and Parrott (24).
The airspeed in the test section could be controlled in steps in the early experiments by changing pulleys on the fan drive, but in later experiments the fan was fitted with a variable-speed motor. The air temperature in the wind tunnel was between 23 and 31 C.

The first gull was trained to fly in the test section by lifting the bird from the floor with a rod until it learned to avoid the rod by fluttering momentarily into the air. After several days of training, the gull had learned to avoid the rod for several minutes by flying, and after several weeks of training, it would fly for 1 hr or more in the tunnel in what appeared to be a normal manner.

The second gull was trained more rapidly by placing it in the test section with the previously trained bird. The naive bird was treated as described above, but within 15 min it learned to fly for a few minutes when accompanied in flight by the trained gull. After 2 weeks of training, the naive gull would fly alone in the test section for 1 hr or more.

Metabolic Measurements

Metabolic rates of resting and flying gulls were determined from oxygen consumption and carbon dioxide production, which, in turn, were calculated from measurements of gas concentrations and flow rates. The caloric equivalent of oxygen was assumed to be 20 kJ/liter (4.7 kcal/liter).

Resting birds were confined in a Plexiglas cylinder 0.76 m long and 0.28 m in outside diameter with a wall thickness of 3.2 X 10^-3 m. The cylinder was kept in a dimly lighted cabinet, the temperature of which was regulated within 0.2 C of 20, 30, or 35 C. A gull was put into the cylinder in midmorning and remained there without food until early evening.

Rates of oxygen consumption and carbon dioxide production were calculated from the concentrations of these gases in the air entering and leaving the cylinder, and the flow rate of air through the cylinder. The lowest rate of oxygen consumption sustained for 1 hr or more during the experiment was used to calculate the resting metabolic rate. Between experiments, the gulls were exposed to summer weather in the outside cage.

Flying birds were fitted with a mask connected to a vacuum system (illustrated in ref. 23) by a flexible vinyl tube 3.5 X 10^-3 m in outside diameter. The mask was made from a piece of flat celluloid folded up and taped to a piece of celluloid centrifuge tube 25 X 10^-3 m in diameter (Fig. 2) and was held on by a rubber band as described in Tucker’s study (22). The mask had a mass of 4.4 X 10^-3 kg. The part of the tube supported by the flying bird had a mass of 6.0 X 10^-3 kg and a length of 0.8 m. Air entered the back of the mask at 0.25-0.33 liters/sec and swept the expired gases into the vinyl tube before they could escape out the back of the mask. The air then passed through a flowmeter (a rotameter), and a sample was pumped through a desiccant (Drierite) to recording carbon dioxide and oxygen analyzers. When the mask was in place on the gull, the pressure within it was never more than 2 mm of H2O below the static pressure outside the mask. The vacuum system regulated the pressure downstream from the flowmeter at 460 mm Hg absolute. Flights during which metabolic measurements were made lasted 0.5 hr or more, and usually two or three measurements of metabolic rate were made each day.

The carbon dioxide analyzer (Beckman infrared analyzer, model 215) was used in the following manner to determine the carbon dioxide production of a flying gull. The concentration of carbon dioxide in the air coming from the mask was recorded while the gull was flying. The respiratory rate was so rapid that breath-to-breath variations in concentration were not recorded. After each flight, the mask was removed from the bird, the end of a plastic tube (PE-100) was placed in the mask, and the opening of the mask was plugged with a porous ball of cheesecloth. Pure CO₂ flowed through a flowmeter and the plastic tube at a rate determined by a needle valve adjusted until the analyzer record came to ca. 10% above the recording obtained from the flying bird. The flowmeter reading was noted and the procedure was repeated; this time the needle valve was adjusted to produce a record slightly below that recorded from the flying bird. Then the rate of carbon dioxide production of the bird was calculated by linear interpolation. This null-balance technique took only a few minutes and did away with the need to measure the carbon dioxide concentration in the air.

FIG. 2. Laughing gull flying in wind tunnel while wearing a celluloid mask.
Mass dropped from 0.420 to 0.383 kg during 3 weeks of the experiment. In the early summer of 1969, measurements were made when the bird had a mass between 0.326 and 0.392 kg. In the winter of 1969, the bird’s mass dropped from 0.420 to 0.383 kg during 3 weeks of experiments. All measurements were made at an airspeed of 10.8 m/sec at the low level of turbulence.

Body mass was measured with a Mettler balance, the systematic error and imprecision of which was negligible.

**Drag of Mask and Tube**

The drag of the tube between the points where it attaches to the mask and reaches the floor of the test section was calculated from the angle (φ) of the tube axis relative to horizontal as the tube hung suspended from the mask and streamed in the wind at various airspeeds. Values of φ were measured with an optical protractor. They had a systematic error of less than 1/2° and an imprecision estimated to be 1/4°.

The value of φ at any point results from the direction of the vector sum of two orthogonal forces on the tube, weight and drag, so that:

\[ D = W \cot \phi \]  

Both W and D increase proportionately with length along a tube of constant diameter and wall thickness, and it follows that such a tube should be straight when streaming in the wind (φ constant at all points along the tube). This condition was observed.

The drag of the mask was measured by mounting a gull model (a stuffed skin) on a one component flight balance and measuring the change in drag as the mask was placed on the gull model or removed at various airspeeds. The flight balance was a vertical brass rod 0.8 m long that passed through the floor of the test section. The base of the rod was equipped with strain gauges that measured the strain caused by the drag of the rod and gull model. The gull model was mounted on the end of the rod and was appropriately oriented in the airstream with its wings tightly folded. The flight balance was calibrated by hanging weights from a thread that ran over a pulley and attached to the gull model so as to apply force in the same direction as the drag vector. The changes in strain were kept so small that they did not significantly alter the position in space of the center of mass of the rod-model system. Changes in strain caused by alterations in the center of mass when the mask was attached or removed were measured and corrected for.

The systematic error of the flight balance was negligible, and the standard error of the value of drag determined at each airspeed was ±2.3 × 10⁻³ newtons (N).

The drag of the mask and tube was partially or completely compensated for during metabolic measurements on flying gulls by tilting the wind tunnel in the wind tunnel so that the air velocity in the test section was inclined upward by 1.5° relative to horizontal (θ = -1.5°). This procedure adds a weight component in a direction opposite to the drag vector and compensates for the drag of the mask and tube at a speed of 8 m/sec. For convenience, flights when θ was -1.5° will be referred to in the text following as level, unless otherwise noted. Metabolic measurements were also made at θ = -2.5° and at θ = -6.5°.

**Wingbeat and Respiratory Rates**

Wingbeat rate was measured by synchronizing a stroboscope with the wingbeats. Respiratory rate during flight was measured by recording from a thermocouple circuit with...
one junction placed in the mask. Each time the bird exhaled, the subsequent warming of the thermocouple could be clearly recorded. Systematic error and imprecision were negligible for both wingbeat rate and respiratory rate.

RESULTS

Behavior

Both gulls learned to fly in the center of the test section so that their flight usually appeared identical to the steady flight of wild gulls. However, at one time or another, both displayed aberrations in flight that were caused by the wind-tunnel environment. They had a tendency to fly at the top of the test section, striking the ceiling (which was covered with a protective net) with their wings at the top of the upstroke. This behavior occurred most frequently during the first 10 min of a flight. However, even after 0.5 hr of flight, the gulls would fly at the top of the test section for a few seconds of each minute.

The erratic flight described above increased in frequency when the tunnel was tilted to negative values of $\theta$. When $\theta$ was $-6.5^\circ$, a gull occasionally would glide for several seconds, remaining motionless relative to the tunnel. Yet most of the time the bird would flap at the top of the test section, working harder than necessary to stay airborne.

One gull, when flying at speeds less than 9 m/sec, developed the habit of continually flying into the net at the front of the test section. Measurements were discarded when the gull behaved in this manner.

When wearing masks, the gulls appeared to flap more laboriously than when they were unmasked. In addition, the gulls without masks would fly for several minutes at a speed of 14 m/sec, but, when wearing the mask, they would not fly faster than 13 m/sec for more than 1 min. The masked gulls usually flew with their beaks open, although their beaks usually were closed in the absence of a mask.

Both gulls exhibited two distinct types of wingbeat, depending on the speed of flight. At speeds below 9 m/sec, the wing tips had a slower downward velocity during the early part of the downstroke than they did at higher flight speeds. This difference caused the birds to have a characteristic snapping motion of their wings during the downstroke when flying at speeds above 9 m/sec. The same snapping motion can be observed in free-living gulls. The change in wingbeat pattern occurred at the same speed at which metabolic rate increased in a stepwise manner as flight speed increased (Fig. 4).

Metabolic Measurements in Flight

Effect of body mass. Thirteen measurements were made on one gull flying at a speed of 10.8 m/sec in low air turbulence with body mass (m) between 0.328 and 0.420 kg (Fig. 3). The linear least-squares relation between log metabolic rate ($P_1$, in watts) and log body mass was:

$$\log P_1 = 1.562 + 0.325 \log m$$

(Se of estimate = $\pm 0.015$), or:

$$P_1 = 36.4 \, m^{0.325}$$

The exponent has 95% confidence limits of 0.05 and 0.60.

The mean mass of both birds for all of the metabolic measurements during level flight was 0.321 kg ($\bar{m} = \pm 0.026$, $n = 112$). One gull was smaller (mean mass = 0.277 kg, $\bar{m} = \pm 0.014$, $n = 25$) than the other (mean mass = 0.329, $\bar{m} = \pm 0.020$, $n = 87$). All of these masses include that of the mask and suspended tube ($1 \times 10^{-2}$ kg).

Effect of speed. Since equation 12 indicates that metabolic rate in flight at a constant speed is proportional to body mass raised to the 0.325 power, all metabolic rates subsequently measured during flight were expressed per mass raised to the 0.325 power. This procedure yields a value that should be insensitive to variations of body mass in an individual bird. Over a speed range from 6.1 to 12.6 m/sec, the mean metabolic rates for each of the two gulls flying level (one gull flew in both high- and low-turbulence air) varied from 23 to 38 w/kg$^{0.325}$ (Fig. 4). At each speed, the metabolic rate of the smaller gull was lower than that of the
A curve (Fig. 4), fitted by least squares to the means of all measurements during level flight had the equation:

\[ P_l/m^{0.285} = (V - 6.0)^2/(5.00 + 27.3) \]  
(13)

(\text{se of estimate} = \pm 3.69, n = 14). Prior to the least-squares fitting procedure, the curve was linearized by using \((V - 6.0)^2\) as the independent variable. Equation 13 represents a parabola with its vertex at 6.0 on the abscissa, and 27.3 on the ordinate.

The rate of change of metabolic rate with speed was slightly but consistently higher between 8 and 10 m/sec than at other speeds (Fig. 4). Although I averaged out this phenomenon in the mean curve described above, it occurred in both gulls and in both level and descending flight (\(\theta = -6.5^\circ\)). It occurred at the same range of speeds where the wingbeats changed from one pattern to another (see Behavior).

Effect of duration. Usually, the metabolic rate of a flying gull was high at the onset of flight and declined 15-20% to a plateau in 15 to 20 min, where it remained until the termination of the experiment after 10 or 20 min more. Occasionally, the metabolic rate was almost constant over the measurement period. The decline in metabolic rate with time correlated with the observation that the gulls flew erratically for the first 10 min of flight (see Behavior).

Effect of angle. Measurements were made only during level flight or flight at negative values of \(\theta\), as neither bird would fly long enough at positive values of \(\theta\) for measurements to be made. One gull, flying at the high-turbulence level, always decreased its metabolic rate at a given speed when the tunnel was tilted from level to \(-6.5^\circ\) (Fig. 4). However, the behavior of the gull suggested that the observed decrement in metabolic rate would have been greater had the gull not struggled at the top of the test section (see Behavior).

Ten measurements were made on the other gull flying at 11.7 m/sec in air at the low-turbulence level in level flight and at an angle of \(-2.5^\circ\). At the latter angle, the bird appeared to fly in the same manner as in level flight, and its mean metabolic rate decreased by 2.9 w/kg \(^{0.39}\). The standard errors of the means for level and descending flight were \(\pm 0.16\) and \(\pm 0.39\), respectively.

Effect of air turbulence. Metabolic measurements were made on one gull flying at the high- and low-turbulence levels at various speeds. At the high-turbulence level, the metabolic rates were more variable and were sometimes lower than at the low-turbulence level (Fig. 4).

Respiratory quotient in flight. Oxygen consumption and carbon dioxide production were measured simultaneously in one bird flying at various speeds. The mean respiratory quotient was 0.71 (SD = \(\pm 0.010\), \(n = 24\)). Between the onset of flight and the first determination of respiratory quotient, 1 or 2 min elapsed. There was no consistent change in respiratory quotient from the beginning to the end of an experiment, which lasted 20 to 30 min.

Metabolic Measurements at Rest

Five metabolic measurements were made on each of two resting gulls at temperatures of 20, 30, and 35 C. Metabolic rate during rest was assumed to be directly proportional to body mass, and was expressed as watts per kilogram to correct for variations in body mass. The linear least-squares equation fitted to the relation between metabolic rate and air temperature \((T_a)\) was:

\[ P_l = (13.4 - 0.14 T_a)m \]  
(14)

(\text{se of estimate} = \pm 0.09, n = 30).

The mean respiratory quotient at rest, measured simultaneously with resting oxygen consumption, was 0.70 (SD = \(\pm 0.050\), \(n = 30\)).

Drag of Mask and Tube

The drag of the mask increased linearly as airspeed increased according to the equation:

\[ D = 0.0013 V - 0.0065 \]  
(15)

Actual measurements of drag were within \(2 \times 10^{-4}\) N of the values given by this equation between 6 and 11 m/sec, but were \(15 \times 10^{-4}\) N high at 13 m/sec.

The tube streamed in the wind at increasingly acute angles to horizontal as airspeed increased from 6 to 13 m/sec, and its total drag increased according to the linear least-squares equation:

\[ D = 0.0128 V - 0.0185 \]  
(16)

(\text{se of estimate} = \pm 0.00235, \(n = 5\)). This equation can be combined with equation 9 to yield an expression for the drag coefficient per unit length of the tube as a function of airspeed. When equation 9 is applied to a cylinder, \(D\) is defined as drag per unit length and \(S\) is defined as the outside diameter of the cylinder. Thus, for the tube:

\[ C_D = 7.65/V - 11.1/V^2 \]  
(17)

The drag coefficient for the tube at the lowest speed \((C_D = 0.97, V = 6 \text{ m/sec}, \phi = 45^\circ)\) approaches that measured by others for a long cylinder oriented with its long axis perpendicular to the direction of airflow. Such a cylinder has a \(C_D\) of 1.0 at a Reynolds number of 2,300 (7), which is the appropriate Re value for the tube attached to the mask. (Reynolds number for a cylinder is defined by equation 7 with \(d\) equal to the outer diameter of the cylinder.)

The total drag added to a flying gull by the mask and tube is given by the sum of equations 15 and 16:

\[ D_m = 0.0141 V - 0.025 \]  
(18)

Wingbeat and Respiratory Rates

The wingbeat rate, measured at speeds between 8.6 and 11.2 m/sec and \(\theta\) between 0 and \(-6.5^\circ\), was virtually constant with a mean value of 3.78 breaths/sec (SD = \(\pm 0.096\), \(n = 21\)). The respiratory rate over the same range of speed and angles was more variable, with a mean value of 2.54 breaths/sec (SD = \(\pm 0.232\), \(n = 36\)). The ratio of the mean wingbeat rate to the mean respiratory rate is 1.5. Respiratory rates were first measured at 10-15 sec after the onset of flight, and did not change consistently before the termination of the experiments, which lasted 2-3 min.

Berger et al. (2) measured a midrange wingbeat frequency and mean respiratory frequency of 4.6 and 2.0, respectively, during flight in the ring-billed gull \((Larus delawarensis, \text{ mass } = 0.376 \text{ kg})\). The ratio of these rates is 2.3.
METABOLISM OF FLYING GULLS

DISCUSSION

The preceding results describe the energetic cost of flight for laughing gulls in a wind tunnel, but does this description apply to birds in nature? To answer this question, several differences between the wind-tunnel environment and that in nature must be evaluated. The differences that I will discuss are: effects due to pressure gradients and proximity of the walls to the test object in the wind tunnel (boundary effects), air turbulence in the wind tunnel, and drag of the mask and tube.

Boundary Effects

The pressure gradients that exist down the length of a wind tunnel and the proximity of the walls of the test section to the test object can produce forces on the test object that do not occur when the object moves through a large volume of still air. These forces have been measured for fixed-wing aircraft (16) but not for flapping-wing aircraft. However, a gliding bird with the dimensions of the gulls used in this study would have corrections for boundary effects that would change its lift and drag by less than 5% (24). Consequently, boundary corrections are assumed to be insignificant in this study.

Turbulence

The metabolic rate during flight was virtually unaffected by changes in the level of turbulence in the wind tunnel. This finding is interesting because the aerodynamic forces on model aircraft or wings in wind tunnels can be profoundly affected by changes in turbulence levels, particularly when the models have Re values (about $10 \times 10^6$) similar to those for the birds in this study. The sensitivity of such models to turbulence can be reduced by roughening the surface of the model. Roughening of the surface can cause transition of the boundary layer from laminar to turbulent flow, and thereby prevent separation of the boundary layer (7, 9, 17, 18, 19).

The drag coefficient of wing models shaped like bird wings can decrease by 20% or more when transition of the boundary layer occurs at the appropriate region (7, 18). In addition, the lift coefficient increases as the drag coefficient decreases, so that the ratio of lift to drag can increase by 50% with transition (18). Feldman (5) measured a 50% increase in lift-to-drag ratio when transition occurred in an appropriate region on the wings of a plaster model of a gull mounted in a wind tunnel.

It is not surprising that the metabolic rates of flying gulls are insensitive to turbulence intensities up to 1.45%. Gulls in nature fly in air with different turbulence levels, and one might expect that they have evolved surfaces that keep the energetic cost of flight as low as possible. The roughness of the feathers on gull wings probably is enough to cause transition of the boundary layer, whether the bird flies in turbulent or nonturbulent air. The overlapping feathers that cover the wing form a series of sharp valleys and rounded peaks, and the relief of these surface features is between $0.5 \times 10^{-6}$ and $1 \times 10^{-6}$ m. This amount of roughness is more than enough to cause transition of the boundary layer at the leading edge of a flat plate exposed to a nonturbulent airflow of 10 m/sec (7).

Extremely high levels of turbulence can increase the energetic cost of flight. The mean metabolic rate of budgerigars flying at 10 m/sec in a highly turbulent closed-circuit wind tunnel (20) was almost twice as high as the mean metabolic rate measured at the same speed in a less turbulent, open-circuit tunnel (22). The turbulence intensities in these tunnels, measured with the techniques described here, were 43% and 4%, respectively.

Drag of Mask and Tube, and Tunnel Tilt

Gulls. The flying gulls were hindered to some extent during metabolic measurements by the aerodynamic drag of the mask and were aided by the tilt of the wind tunnel. In this section I will develop equations that correct the measured power expenditures of the flying gulls for these two effects.

When a bird wears a mask, its drag increases, and it must increase thrust to maintain its position in the test section. The bird also must change its thrust when the wind tunnel is tilted from the horizontal by angle $\theta$. If $D_m$ is the drag added by the mask and its attached tube, the total increase in the magnitude of thrust to compensate for mask and tube drag and tunnel tilt is given by:

$$\Delta T = D_m + W \sin \theta \quad (19)$$

The increase in power output ($P_o$) required to provide this increase at flight speed $V$ is:

$$\Delta P_o = AT V \quad (20)$$

The amount that a bird must increase its metabolic rate (power input, $P_i$) to achieve this increase in $P_o$ depends on the partial efficiency ($E_p$, equation 6), so that

$$\Delta P_i = (D_m + W \sin \theta)V/E_p \quad (21)$$

If $E_p$ can be determined, equation 21 can be solved, and $\Delta P_i$ can be subtracted from the measured power input of the gulls flying in the wind tunnel to get a value for the power input of a gull in level flight and unhindered by the drag of the mask.

Partial efficiency can be determined from measurements of $P_i$ of gulls flying in a level and a tilted tunnel. I encountered difficulty in making appropriate measurements because the gulls changed their flight pattern when the tunnel was tilted by several degrees (see Behavior). However, one gull flew at 11.7 m/sec in what appeared to be an unchanged manner as the tunnel was tilted from $\theta = -1.5^\circ$ to $\theta = -2.5^\circ$. The change in power output of the bird as the tunnel tilted was:

$$\Delta P_o = WV \Delta \sin \theta \quad (22)$$

where $\Delta \sin \theta = \sin 1^\circ$. The change in power input was 2.9 W/kg. These data indicate an $E_p$ of 0.3 for a bird of mean mass in this study (0.322 kg).

Partial efficiency varies with flight speed in the only other flying animal for which it has been measured, the budgerigar (22). In this bird, $E_p$ varied between 0.19 and 0.28 at flight speeds between 5 and 13 m/sec (Table 1). Although I have no data on changes in $E_p$ with flight speed for gulls, changes in $E_p$ such as those measured for budgerigars have a relatively small effect on the values of power output corrected for mask drag and tunnel tilt. The equation that de-
Gerigars have been measured (22). Since the drag of the gull mask is
be calculated with equation 21, since $E_p$ values for flying bud-
small (less than 15% of the drag of the tube), and the bud-
the mask and tube in a previous study of the flight ener-
ment of power input due to the drag of the tube then can
speed by substituting equation 9 into equation 17. The incre-
the drag of the mask in the budgerigars can be neglected.

The CD values for the tube attached to the budgerigar mask is only 60% of that for the gull mask,
attached to the gull mask. Although the Re value (1,400)
mask should be about the same as those for the tube at-
level flight. The term for nonlevel flight is:

$$\Delta P_I = WV \sin \theta/E_p = 9.81 \, \text{mV} \sin \theta/E_p \quad (25)$$

The foregoing analysis shows that the amount of power ($P_I$) that the masked gulls expended during level flight in the wind tunnel is close to the amount ($P_I^*$) calculated for $\theta = 0$ after correcting for the drag of the mask. For example, $P_I^*$ (equation 24) for a gull with a mass of 0.322 kg is 2% greater than $P_I$ (equation 13) at 6 m/sec. At 12 m/sec, $P_I^*$ is 10% less than $P_I$.

**Budgerigars.** The measurements of drag of the mask and tube for the gulls make it possible to correct for the drag of the mask and tube in a previous study of the flight energetics of budgerigars (22). Since the drag of the gull mask is small (less than 15% of the drag of the tube), and the bud-
gerigar mask fitted even more closely than the gull mask, the drag of the mask in the budgerigars can be neglected. The $C_D$ values for the tube attached to the budgerigar mask should be about the same as those for the tube attached to the gull mask. Although the Re value (1,400) for the tube (od, 2.1 X $10^{-3}$ m; length, 0.15 m) attached to the budgerigar mask is only 60% of that for the gull mask, the $C_D$ values for cylinders do not change appreciably over this range of Re values (7). Thus, the drag of the tube for the budgerigar mask can be calculated as a function of speed by substituting equation 9 into equation 17. The increment of power input due to the drag of the tube then can be calculated with equation 21, since $E_p$ values for flying bud-
gerigars have been measured (22).

The power inputs of budgerigars in level flight are re-
duced 2–18% when the increment of power input due to
drag of the tube is subtracted from the measured power input (Table 1). After correcting for tube drag, the power inputs for a 0.035-kg budgerigar flying level at speeds between 5.3 and 13.3 m/sec are given by the parabolic equation:

$$P_I^* = \left[0.180 \left( V - 9.7 \right)^2 + 3.52 \right] m_{0.325}$$

This equation fits the data in Table 1 within 4% or better except at the slowest speed of 5.3 m/sec, where it is 12% too high.

### Table 1. Correction of budgerigar metabolism in level flight for mask and tube drag

<table>
<thead>
<tr>
<th>Flight Speed, m/sec</th>
<th>Mean Measured Power Input, J</th>
<th>$E_p$</th>
<th>Corrected Power Input, J</th>
</tr>
</thead>
<tbody>
<tr>
<td>5.3</td>
<td>6.34</td>
<td>.27</td>
<td>6.79</td>
</tr>
<tr>
<td>6.7</td>
<td>5.40</td>
<td>.28</td>
<td>5.25</td>
</tr>
<tr>
<td>7.8</td>
<td>4.45</td>
<td>.20</td>
<td>4.10</td>
</tr>
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<td>9.7</td>
<td>4.27</td>
<td>.19</td>
<td>3.67</td>
</tr>
<tr>
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<td>.19</td>
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<tr>
<td>13.3</td>
<td>6.67</td>
<td>.28</td>
<td>5.87</td>
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and exposure of the thinly feathered undersides of the wings and sides of the thorax in flight.

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REFERENCES


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