Oxygen Consumption of a Flying Bird

Abstract. *Budgerygahs* (Melopsittacus undulatus) *flew with a minimum oxygen consumption of 38 milliliters per gram-hour at each of three speeds between 19 and 33 kilometers per hour in a recirculating wind tunnel. An oxygen debt accumulated in the first minute of flight and was repaid in the minute following cessation of flight. Frequency of wing-beat was independent of flight speed. The data suggest that flying budgerygahs have a higher cardiac output per kilogram of body weight than mammals and that flight muscle of the budgerygah is among the most metabolically active tissues known.*

Various estimates have been made of the energetic cost of bird flight (*1*), but measurements in terms of oxygen consumption are available only for hummingbirds during hovering (*2*). This report presents measurements of oxygen consumption in budgerygahs during horizontal flight at various speeds.

Oxygen consumption was measured while birds were flying for 2 minutes in a sealed wind tunnel in which the air was recirculated (Fig. 1). Air was driven at speeds between 19 and 33 km/hr by a four-wing Dayton fan (diameter, 25 cm; pitch, 31 deg). A 2-hp electric motor drove the fan through a system of belts and pulleys. Birds flew in a space 30 cm square and 34 cm long.

Air flow in the tunnel was both nonhomogeneous and turbulent. Air speed, measured with an anemometer 7 cm in diameter, varied as much as 6 percent from top to bottom of the space where the birds flew. Turbulence was recorded with a pitot tube connected to a Sanborn 268B differential pressure transducer and an oscillograph. In midstream at 25 km/hr the pitot tube registered a mean pressure differential of about 0.4 cm-water, but this value changed erratically between 0.2 and 0.6 cm-water approximately 30 times each second. Three or four times a second, the pitot tube registered abrupt pressure differentials as high as 1 cm-water, but such values lasted less than 10 msec.

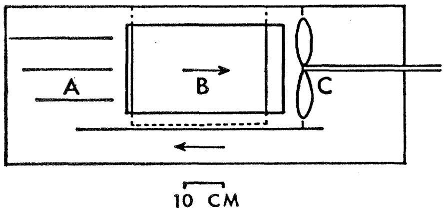

Fig. 1. Cross section of the wind tunnel used in this study. Arrows show the directions of air flow. Adjustable vanes (*A*) determine the air speeds at different heights in the working section (*B*). The working section is bounded by a plexiglas window and an electrified grid. The fan shaft (*C*) enters the tunnel through an air tight O-ring seal.

Oxygen content of air drawn from the wind tunnel was continuously recorded by a Beckman paramagnetic oxygen analyzer. This instrument gave a full scale response for a change of 0.001 in fractional content of oxygen. A diaphragm pump moved air at 12 liter/hr from the wind tunnel through a desiccant and a flow meter to the oxygen analyzer. Leakage from the room replaced air removed from the wind tunnel by the pump, but the tunnel was sealed tightly enough to prevent measurable diffusion of air between the inside and outside. Oxygen consumption (expressed in liters per hour at standard temperature and pressure) was calculated from the oxygen analyzer record with the equation

$$\text{oxygen consumption} = \frac{-PV}{2.78T}\,\frac{dF}{dt} + f(0.2094 - F)$$

where P is atmospheric pressure (mm-Hg); V, volume of wind tunnel (157 liters); T, °K; F, fractional concentration of oxygen in dried air from wind tunnel; t, time; and f, rate of leakage of room air into wind tunnel (12 liter/hr). This equation is exact for a respiratory quotient of 1, but large changes in respiratory quotient do not affect it significantly.

Volume of the wind tunnel was calculated after injecting 100 ml of oxygen and noting the change in F. Three determinations gave values of 159, 156, and 156 liters.

Oxygen (100 ml) was infused into the wind tunnel at a rate of 1.15 liter/hr to demonstrate that the oxygen analyzer accurately measured the rate of change of oxygen content in the tunnel. In three trials the oxygen analyzer records indicated infusion rates of 1.12, 1.15, and 1.19 liter/hr. These values were close to some of those observed during flight experiments, although opposite in sign.

Frequency of wing-beat was determined from photographs made with a 16-mm Bolex camera running at 64 frames per second and synchronized to a Chadwick-Helmuth stroboscope.

The two budgerygahs used in these experiments were purchased at a local pet store and had mean weights of 42 and 32 g. They were trained to fly in the wind tunnel with the use of an electrified grid on the floor and at the ends of the working section. At the lowest flight speed of 19 km/hr the birds hovered with their bodies inclined about 30 deg from horizontal and their feet partly retracted, at 25 km/hr the body angle was 17 deg, and at 33 km/hr it was 5 deg. It was not feasible to drive the tunnel at higher speeds. These budgerygahs could fly at least 52 km/hr in a different open-circuit wind tunnel.

Oxygen consumption rose abruptly after the onset of flight, was constant during flight, and dropped abruptly to about the initial level when flight stopped (Fig. 2). The time lag between onset of flight and attainment of constant oxygen consumption represents accumulation of an oxygen debt, since infusion experiments demonstrated that the oxygen analyzer was capable of recording abrupt alterations in rate of change of oxygen content as perfect square waves on the time scale used in this study. The mean time over which an oxygen debt accumulated was 44 seconds (S.D., 17; *N*, 16). The lag between cessation of flight and attainment of constant oxygen consumption represents repayment of the oxygen debt.

The magnitude of the oxygen debt can be estimated from the area between the measured curve, the vertical line marking the cessation of flight, and a horizontal line drawn through the lowest rate of oxygen consumption maintained after a flight. The mean oxygen debt was 0.158 ml of oxygen per gram (S.D., 0.049; *N*, 16). In two-thirds of the records, the oxygen debt was repaid a minute or less after cessation of flight.

Measurements on budgerygahs suggest that anaerobic metabolism could be the major immediate energy source for the flights many birds carry out in their natural environments. If 38 ml of oxygen $(\text{g-hr})^{-1}$ represents the minimum energy requirement for flight at 33 km/hr, then accumulation of an oxygen debt of 0.158 ml/g would provide this energy for 15 seconds and allow a flight of 137 m; the oxygen debt could be repaid in less than 1 minute. Many birds in nonmigratory seasons rarely fly farther, or more frequently, than these figures indicate.

Oxygen consumption in flight varied

Table 1. Mean oxygen consumption of two budgerygahs during flight. Fourteen measurements were made on each bird at each speed.

Wt. of bird (g)	Mean oxygen consumption [ml (g-hr)$^{-1}$ ± S.D.] at three flight speeds (km/hr)		
	19	25	32
	Bird No. P1		
42	41.0 ± 2.28	41.0 ± 3.59	38.7 ± 1.41
	Bird No. P4		
32	48.3 ± 5.75	45.1 ± 3.79	42.8 ± 3.44

widely, but the lowest sustained rates at each speed were near 38 ml (g-hr)$^{-1}$ (Fig. 3). Mean rates of oxygen consumption decreased as flight speed increased (Table 1). Bird P4 used significantly more oxygen than bird P1 at both the highest and the lowest speeds.

A flying bird should travel as far as possible on a given amount of fuel, and "flight economy" is expressed as the ratio of flight speed to oxygen consumption. Since the minimum oxygen consumption in flight is constant at all speeds used in this study, flight economy increases linearly with flight speed, at least to 33 km/hr.

Measurements of oxygen consumption reveal that budgerygahs in flight must have higher heart rates or higher stroke volumes per kilogram of body weight, or both, than are known in mammals. Essentially all of the oxygen consumed is transported from the lungs to the tissues by the cardiovascular system. Oxygen transport is described by the equation, oxygen consumption = heart rate × stroke volume × A-V difference. The last factor is the difference in oxygen content of arterial and mixed venous blood. This difference cannot be greater than the oxygen capacity of the blood, which is less than 20 ml of oxygen per 100 ml of blood in the small birds that have been investigated (*3*). Thus, the cardiac output (heart rate × stroke volume per kilogram of body weight) of a flying budgerygah with an oxygen consumption of 45 ml (g-hr)$^{-1}$ should be greater than 225 liters of blood (kg-hr)$^{-1}$. If the heart of the bird beats 1000 times per minute, stroke volume would have to be at least 3.75 ml of blood (beat-kg)$^{-1}$.

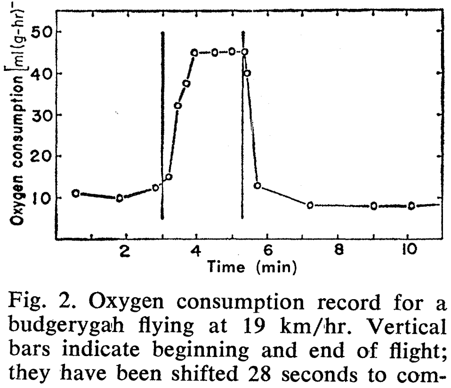

Fig. 2. Oxygen consumption record for a budgerygah flying at 19 km/hr. Vertical bars indicate beginning and end of flight; they have been shifted 28 seconds to compensate for time required for air sample to move from tunnel to oxygen analyzer.

Small mammals have stroke volumes between 0.5 and 1.0 ml (beat-kg)$^{-1}$ (*4*), and, judging from humans and dogs (*5*), this value may double during exercise. If a budgerygah had a stroke volume of 2.0 ml (beat-kg)$^{-1}$, it would need a heart rate of at least 1875 beats per minute. The highest heart rates I know of in vertebrates do not exceed 1320 beats per minute (*6*).

Frequencies of the wing-beat of the two budgerygahs at all flight speeds varied less than 6 percent from a mean value of 13.6 beats per second. Greenewalt (*7*) observed that the wing-beat frequencies of other birds also are constant at various flight speeds and explained this by considering flight systems as mechanical oscillators driven at their resonant frequencies. Such a resonant system attains a given amplitude of oscillation with a minimum energy input and could be a device for conserving energy in flying animals. Greenewalt also showed that the wing-beat frequencies of insects and birds have an empirical continuous relation to wing length in a manner consistent with the theory of mechanical oscillators. The budgerygahs used in this study had a mean wing length of 96 mm. This corresponds to a predicted wing-beat frequency of 12.5 beats per second, which is in good agreement with the observed value.

The only other direct measures of oyxgen consumption available for birds in flight are those of Pearson and Lasiewski for hovering hummingbirds (*2*). By considering the proportion of time spent in hovering and at rest during the measurement period, these authors estimated values of oxygen consumption during hovering as high as 147 ml (g-hr)$^{-1}$. However, Lasiewski reported a mean rate of only 42 ml of oxygen (g-hr)$^{-1}$ during 35 minutes of continuous hovering by a 3-g Costa's hummingbird (*Calypte costae*). This value is within the range of those for flying budgerygahs.

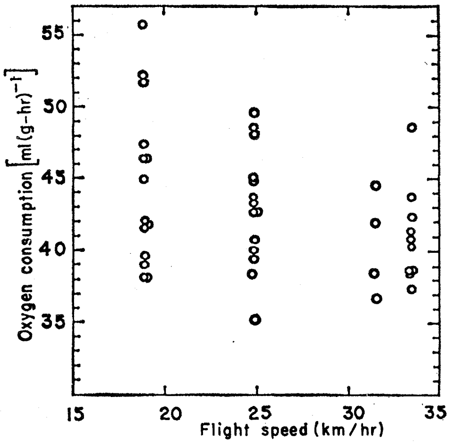

Fig. 3. Oxygen consumption of two budgerygahs during flight at various speeds.

The oxygen consumption measurements during flight indicate that budgerygah flight muscles are among the most metabolically active tissues known. A 40-g bird in flight uses as much as 2000 ml of oxygen per hour. When sitting quietly in the wind tunnel, the bird consumes about 320 ml of oxygen per hour. The difference in these values should be close to the increase in oxygen consumption of the flight muscles. Since the flight muscles of budgerygahs make up 26 percent of the body weight (*8*), I estimate that the flight muscles increased their oxygen consumption by 2.7 ml per gram of muscle per minute. This value indicates that the flight muscle of birds consumes oxygen at a rate comparable to that of insect flight muscle, which uses between 1.4 and 7.3 ml of oxygen per gram of muscle per minute during flight and is said to be the most active tissue known (*9*).

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References and Notes

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