

THE METABOLIC COST OF FLIGHT IN UNRESTRAINED BIRDS

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SUMMARY

Oxygen consumption and carbon dioxide production were measured during flight in unrestrained starlings by a new method. Mean RQ after the first 30 min of flight was 0.69 ± 0.08 (\pm S.D.). Mean rate of carbon dioxide production was 19.7 ± 2.2 ml CO_2 /min, which corresponds to a metabolic rate of 8.9 ± 1 W. Metabolic rate during flight did not change significantly over a range of air speeds from 8 to 18 m/s and birds would not fly at speeds outside of this range. Current theories of bird flight predict a large change in metabolic rate over the same range of speeds. Wingbeat frequency was constant at 12 ± 0.5 Hz. Wingbeat amplitude reached a minimum at a speed of 14 m/s and increased at both higher and lower speeds. Angle between the body and horizontal was least at high speeds and increased at low speeds. As existing theories do not take into account the change of drag resulting from changes in body attitude, this may be a cause of the discrepancies between theory and observation.

INTRODUCTION

Numerous methods have been employed to determine the metabolic cost of flight in birds and the results have differed widely (Nisbet, 1967; Berger & Hart, 1974; Torre-Bueno, 1975). Tucker (1966) used indirect calorimetry to determine the metabolic rate of budgerigars during 2 min flights in a small air-tight wind-tunnel. He later modified this method by using a mask and sampling tube to collect expired gas. This modified method has been used on budgerigars (Tucker, 1968), laughing gulls (Tucker, 1972) and fish crows (Bernstein, Thomas & Schmidt-Nielsen, 1973). Recently, Greenewalt (1975) has questioned this work on the grounds that Tucker's estimate of the increase in the cost of flight due to the mask and tube was inadequate and the method would therefore overestimate the work of flight.

This paper reports the first measurements of oxygen consumption and carbon dioxide production in unrestrained birds during long flights in a low turbulence environment.

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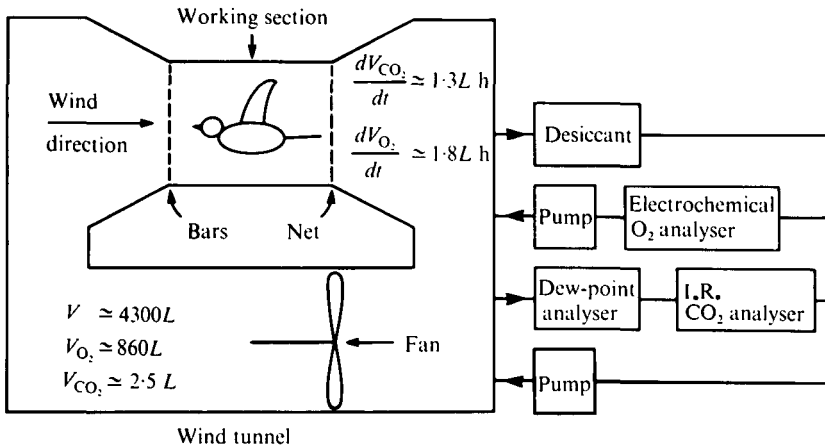


Fig. 1. Diagram of the wind-tunnel and associated instruments.

MATERIALS AND METHODS

The principle of the method is to measure the change in P_{O_2} and P_{CO_2} caused by the bird's respiration in an air-tight closed-circuit wind-tunnel. The tunnel has a volume of approximately 4300 l and is sealed air-tight by gaskets on all joints, a shaft seal on the fan drive-shaft, and an O-ring on the door. The working section in which the birds fly is 71 cm wide, 40 cm deep and 92 cm long. It has 1 mm bars at the upstream end and a net at the downstream end to keep the bird out of the fan. It is illuminated from the upstream end to keep the bird orientated phototactically and the room is kept dark so that the bird would not be attracted towards the transparent side wall. The wind speed is controlled by a set of adjustable vanes upstream of the fan and can be continuously varied from 5.5 to 19 m/s. The tunnel is described and illustrated in Linderoth (1975).

Wind speed was measured with a pitot tube and slant tube manometer with an uncertainty of 0.15 m/s, set by the resolution of the manometer. Turbulence and non-uniformity of wind speed were checked with a hot-wire anemometer. The turbulence was less than 2.2% at all wind speeds, and the velocity was uniform within 5% at all points more than 5 cm from the wall. Velocities as measured by the pitot tube and the hot-wire anemometer were compared to establish that there was no discrepancy between them.

The birds used were wild starlings (*Sturnus vulgaris*) taken as adults with mist nets or traps. They were kept in outdoor aviaries $5 \times 1.2 \times 2.2$ m, 3–5 birds to a cage, and fed a diet of beef liver, ground dog-chow, and mealworms *ad lib*. Birds were trained to fly by tossing them upstream in the wind-tunnel with their feet taped so they could not grasp the bars. If a bird attempted to land it would be chased by rapping the walls of the wind-tunnel or waving a hand or stick in the direction it was turning. A bird which landed repeatedly was quickly removed from the tunnel so that it would not become accustomed to being in the tunnel when not flying. Birds were trained until they would fly 90 min without being chased, before they were used in experiments. Training took 1–2 months and only 5 out of approximately 100 birds which began training reached the 90 min criterion. Training methods are described more fully.

Torre-Bueno (1975, 1976). In well-trained birds the flight pattern consisted of bursts of flapping interspersed with brief glides as is typical of starlings in the wild.

Partial pressure of oxygen in the tunnel was measured with an electrochemical oxygen analyser (Applied Electro-chemistry S-3A). Gas was drawn from the tunnel, passed through a drierite column and the gas analyser, and returned to the tunnel with a pump. Carbon dioxide was measured in a separate loop which consisted of a dew-point hygrometer, an infra-red gas analyser (Beckman IR-215), and a pump. The apparatus is illustrated diagrammatically in Fig. 1. The resolution was 0.005% for oxygen and 0.001% for carbon dioxide. Temperature was measured with a thermistor in the tunnel. Temperature was kept at between 10 and 14 °C as the birds flew best within this temperature range. Partial pressure of water was less than 660 Pa (5 mmHg) during all flights.

The system was calibrated by introducing known volumes of pure oxygen or carbon dioxide with a volumeter. Measurements with the carbon dioxide analyser were corrected for drift by measuring its response to pure nitrogen and 0.1% CO₂ in nitrogen after each reading. The system was checked for spurious response by running it without a bird. There were no detectable changes in P_{O_2} and P_{CO_2} in the absence of the bird. Changing the wind speed had no effect on the accuracy or the sensitivity of the system. Two other tests involved burning a known quantity of alcohol or infusing CO₂ at approximately the rate the bird produced it. Both of these methods agreed with the volumeter calibration. The tunnel was checked for leaks by raising F_{CO_2} to 0.1% and measuring the rate of decline towards room F_{CO_2} . The error in the rate of gas exchange due to leakage from the tunnel was never greater than 2% and was less than 0.5% on most flights.

The overall uncertainty in the rate of oxygen consumption or carbon dioxide production depends on the duration of the flight. In a 1 h flight it was $\pm 12\%$ for oxygen and $\pm 4\%$ for carbon dioxide, and was set principally by the resolution of the gas analysers.

During gas-exchange measurements the procedure was to start the wind-tunnel, toss the bird in with its feet taped, seal the door, and read P_{O_2} and P_{CO_2} every 15 min for at least 90 min. All data presented relate to the 30th to 90th minute of flight, since there are initial transients in body temperature and respiration (Torre-Bueno, 1976, 1977), and it is the steady-state values which are of interest in this context.

At the end of 90 min P_{CO_2} never exceeded 0.1% and P_{O_2} was never less than 20.5%. This is not sufficiently different from the standard atmosphere (20.9% O₂, 0.04% CO₂) to affect respiration.

Wingbeat rates were measured photoelectrically. The birds were illuminated from the front by 12 V d.c. lights. Since the light scattered to the sides varied with the position of the wings the rate of variation of the intensity of side-scattered light indicated the wingbeat frequency. Side-scattered light was detected by an array of photocells and the photocell signal filtered with a pass-band of 5–20 Hz to remove low-frequency transients due to the bird's motion relative to the photocells and 60-cycle noise due to stray a.c. lights. The filtered signal was recorded on magnetic tape and analysed with a Schmidt-trigger and a frequency-to-voltage converter which was calibrated with a known frequency source. The uncertainty of this measurement was 0.5 Hz limited principally by the duration of the bursts of flapping.

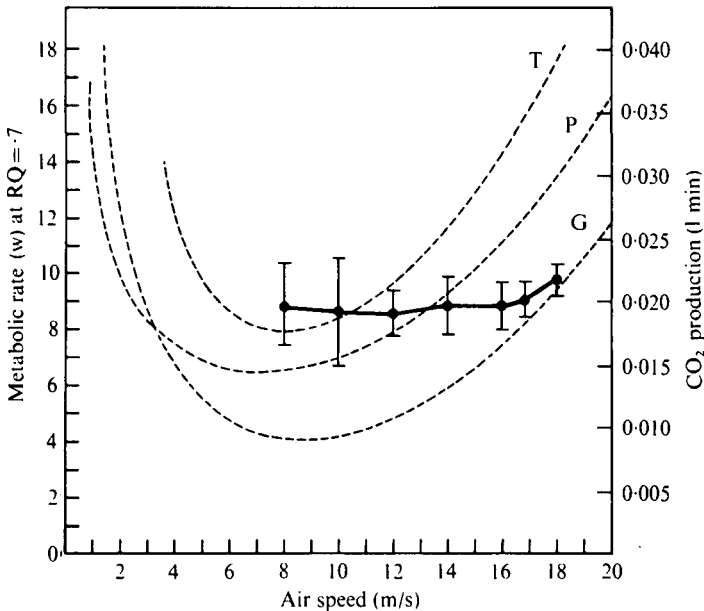


Fig. 2. Metabolic rate as a function of air speed in three starlings (●—●; bars indicate ± 1 s.d.). ---, Predictions of theories by Tucker (1974) (T), Pennycuick (1975) (P), and Greenewalt (1975) (G).

Body attitude during flight was measured by photographing the flying bird from the side. The attitude was defined as the angle between a line from the base of the neck to the base of the tail and the horizontal. Attitude was considered positive when the head was up. The uncertainty of a single attitude measurement was determined by the degree to which the reference points could be exactly located on the photograph, and was about $\pm 5^\circ$.

The wingbeat amplitude was estimated by illuminating a bird with a strobe light and sketching the upper and lower limits of the wingbeat cycle. The angle between the highest and lowest position was read from the sketch with a protractor. The accuracy of the method was checked by applying it to arbitrarily drawn angles and comparing the results to direct measurements, the uncertainty was less than $\pm 15^\circ$.

RESULTS

Fig. 2 shows the rate of CO₂ production as a function of flight speed (the power curve) for 72 flights by three starlings (mean mass 72.8 g). The mean rate of CO₂ production over all flights was 19.7 ± 2.2 (\pm s.d.) ml CO₂/min; there was no significant dependence of CO₂ production on flight speed. The data are reported in terms of CO₂ production because there were more CO₂ measurements and their variance was lower than the O₂ measurements.

The mean RQ after the first 30 min of flight for the 28 flights in which both O₂ and CO₂ were measured was 0.69 ± 0.08 . In a study of respiration during flight in the starling the RQ determined by sampling air-sac contents was 0.71 ± 0.02 (Torre-Bueno, 1977). An RQ of 0.7 was therefore used to convert the rate of CO₂ production to metabolic rate in watts as is shown in the left ordinate in Fig. 2.

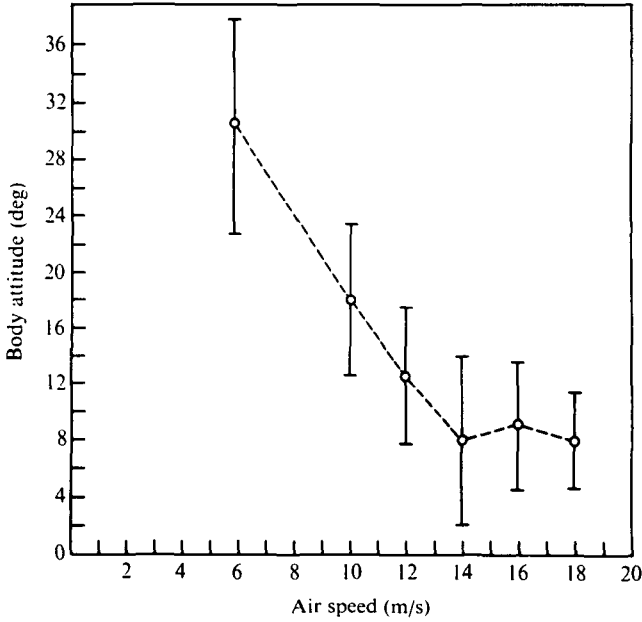


Fig. 3. Body attitude during flight as a function of air speed. Body attitude is given as the angle between a reference line from the base of the neck to the base of the tail and the horizontal. Vertical bars indicate ± 1 S.D.

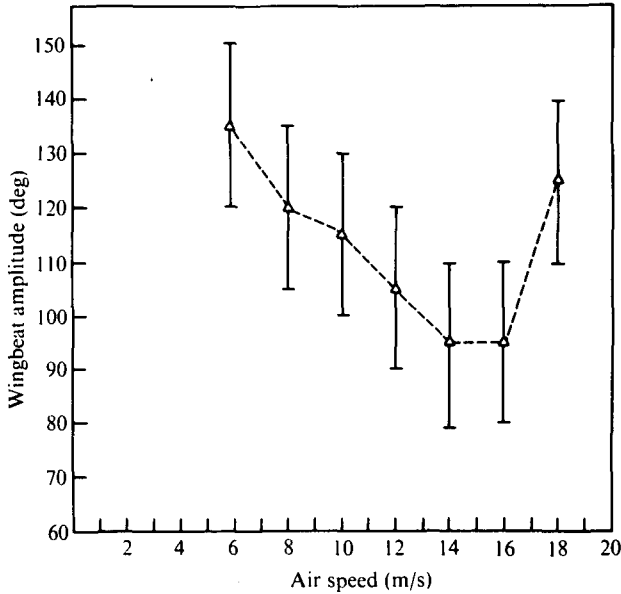


Fig. 4. Wingbeat amplitude during flight as a function of airspeed. Vertical bars indicate ± 1 S.D.

The highest speed at which a starling could be induced to fly for 90 min was 18 m/s and the lowest speed was 8 m/s. At higher speeds the birds would repeatedly hit the rear net and at lower speeds they would land regardless of how vigorously they were chased.

Wingbeat rate was quite constant at 12 ± 0.5 Hz at all speeds between 8 and 18 m/s. The body attitude as a function of flight speed is shown in Fig. 3. At low speeds the body was increasingly tilted up and the feet were trailed. The 'normal' attitude, with the body nearly level (the reference line at $+8^\circ$) and the feet tucked up, was maintained at speeds of 14 m/s and up. In a study in which starlings were given a choice of flight speeds, 13.5 m/s was the preferred speed (Torre-Bueno, 1975). One bird was forced to fly briefly at 6 m/s. At this speed the feathers on the back of the neck were lifted, presumably because of flow separation due to the disruption of streamlined flow. Wingbeat amplitude as a function of air speed is shown in Fig. 4. It reached a minimum at 14–16 m/s and increased at both higher and lower speeds.

DISCUSSION

The dotted lines in Fig. 3 represent the power curves predicted by three models, those of Pennycuik (1975), Tucker (1974) and Greenewalt (1975), for a bird of the shape, size and mass of the starlings. The most striking difference between theory and observation is that all three theories predict an increase in the metabolic rate with increasing speed, whereas only a slight and non-significant increase was observed in the present experiments. Tucker (1968) found that the power curve for the budgerigar is strongly U-shaped. He also showed that the power curve for a gull increases 30% between 6 and 12 m/s (Tucker, 1972). However, fish crows like starlings have an essentially flat power curve (Bernstein *et al.* 1973). The models predict an increase in metabolic rate with windspeed because all three have a term for the power necessary to overcome parasite drag, which includes $C_{D_p}V^3$, where C_{D_p} is the coefficient of parasite drag and V is the velocity. Greenewalt and Tucker make C_{D_p} a decreasing function of Reynolds number, and thus velocity, which reduces the effective exponent of the velocity to 2.7 in Greenewalt's model and 2.5 in Tucker's. Pennycuik assumes that C_{D_p} is independent of velocity. The coefficient of parasite drag is a function of an object's shape and orientation and the Reynolds number of the flow (Von Mises, 1945). For an object shaped like a bird, the C_{D_p} should increase with increasing attitude relative to the flow. Measurements of the dependence of C_{D_p} on attitude for bird-shaped objects are not available in the relevant range of Reynolds numbers (approx. 50000). However, at lower Reynolds numbers, Weis-Fogh (1956) found that for a locust a 15° change in attitude led to a doubling in C_{D_p} and at higher Reynolds numbers experiments with a model airship found that a 10° increase in attitude increased C_{D_p} by 1.8 times (Zahm, Smith & Loudon, 1925). It therefore seems reasonable to believe that for a starling the attitude effect would make the coefficient of parasite drag decrease more rapidly with speed than either Greenewalt or Tucker's models allowed. This would result in a lower effective exponent for the velocity and a relatively flat power curve, as was observed.

The flat power curve observed raises another question. It has been generally assumed that the maximum and minimum airspeeds are set by the intersection of the power curve with some maximum metabolic rate (Pennycuik, 1975). To apply this explanation to the data on starlings it would be necessary to assume that the power curve is flat over a wide range and increases abruptly at 8 and 18 m/s. Such an explanation is unlikely and it becomes necessary to consider other possible mechanisms which might limit the range of speed the starling is capable of. One obvious possibility

is the wingbeat amplitude. The wingbeat amplitude cannot exceed 180° and Pennycuick & Parker (1966) found that in a pigeon the maximum range of motion was 142° . The data in Fig. 4 show that as a starling flies either faster or slower than some optimum speed it must increase the wingbeat amplitude, presumably for aerodynamic reasons. It is therefore possible that the upper and lower speed limits are set by mechanical factors, i.e. a starling may not be able to beat its wings through a large enough amplitude to fly faster than 18 m/s or slower than 8 m/s.

Amplitude limits to the wingbeat are not the only possible explanation. For instance, it is conceivable that flight speed is limited not by considerations of propulsion but by the bird's ability to maintain a stable flight attitude at extreme speeds. The problems of stability and control in a flying bird are largely untouched.

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