

RESPIRATORY AND CARDIOVASCULAR RESPONSES OF THE PIGEON TO SUSTAINED, LEVEL FLIGHT IN A WIND-TUNNEL

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SUMMARY

1. Five pigeons were trained to fly in a boundary-layer wind-tunnel at a velocity of 10 m s^{-1} for at least 10 min, and a number of respiratory and cardiovascular variables were recorded. For comparison, heart rate, respiratory frequency and E.M.G. from the pectoralis major muscles were also recorded, using radio-telemetry, from free-flying pigeons.

2. For the flights in the wind tunnel there were immediate increases in respiratory frequency and heart rate upon take-off; these variables continued to increase during the flight, eventually becoming on average $411 \text{ breaths min}^{-1}$ ($20 \times$ resting) and $670 \text{ beats min}^{-1}$ ($6 \times$ resting) respectively. There was a 1:1 relationship between ventilation and wing beat. Oxygen uptake and carbon dioxide production reached their highest values of $12.5 \times$ and $14.4 \times$ resting respectively within 1 min of take-off and then declined to steady levels of $200 \text{ ml kg}^{-1} \text{ min S.T.P.D.}$ ($10 \times$ resting) and $184 \text{ ml kg}^{-1} \text{ min S.T.P.D.}$ ($10.7 \times$ resting) 4 min after take-off. If allowances are made for the weight and drag of the \dot{V}_{O_2} mask and tubes, these stable values are at least 12% higher than would occur in an unloaded bird. Body temperature rose steadily after take-off, reaching a stable value of 43.3°C , which was 2°C above resting, after 6 min of flight. There was a $1.8 \times$ rise in $a - \bar{v}_{O_2}$ content difference and little change in cardiac stroke volume during flight, so that the rise in heart rate was the major factor in transporting the extra O_2 to the active muscles. Respiratory quotient rose from 0.85 at rest to 0.99, 30 s after take off, and then fell to 0.92 after 7 min of flight. Blood lactate rose to $59.8 \text{ mg}\%$ ($6.5 \times$ its resting value).

3. Comparisons with the free-flying birds indicated that the pattern of flight in the wind tunnel was somewhat abnormal, especially at the beginning of a flight, and this may account for the value of \dot{V}_{O_2} being higher at the start of a flight and then declining to a steady value as the flight progressed.

4. Upon landing, heart rate, \dot{V}_{O_2} , \dot{V}_{CO_2} and body temperature began to fall immediately, and within 2 min, heart rate, \dot{V}_{O_2} and \dot{V}_{CO_2} had returned to the 'tunnel on' resting values. Respiratory frequency increased upon landing and its decline closely matched the fall in body temperature. R.Q. rose above unity immediately upon landing as CO_2 was removed in excess of its

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metabolic production, and then fell below the resting value as CO_2 was retained, presumably to maintain acid/base balance during the metabolism of lactic acid.

INTRODUCTION

Birds cannot only travel long distances at high speeds (Lefebvre, 1964; Tucker & Schmidt-Koenig, 1971) but they can also do so at high altitudes where the environmental oxygen tension is low (Tucker, 1975). Although the physiological adaptations necessary to sustain such flight must be remarkable, the study of the responses to flight in birds has been slow to develop because of a lack of appropriate techniques. Indirect estimates of metabolic rate during long flights have been made (Lefebvre, 1964), but information on the accompanying respiratory and cardiovascular changes has been largely restricted to flights of short duration, usually of a few seconds (Tomlinson & McKinnon, 1957; Eliassen, 1963; Hart & Roy, 1966). The use of a wind-tunnel, however, allowed Tucker (1966, 1968, 1972) to obtain more direct measurements of metabolic rate, respiratory frequency and wing-beat frequency during flights of up to 30 min duration. Tucker (1972) went to great lengths to quantify, and where necessary to take into account, the effects of turbulence in the tunnel and the drag of tubes and leads so that the data obtained bore as close a relationship as possible to natural conditions.

Work on humans has indicated that the ability to perform great feats of physical endurance is to a large extent related to a high capacity for carrying out aerobic metabolism (Margaria, Cerretelli, Aghemo & Sassi, 1963). As this capacity is indicated by the individual's maximum oxygen consumption, it is clear that a measure of oxygen uptake is of central importance when studying the responses of an animal to exercise. Maximum oxygen uptake appears, in humans at least, to be limited by the rate of oxygen transport by the circulatory system (Rowell, 1974). The object of the present investigation was initially to measure the oxygen consumption and respiratory responses of pigeons trained to fly in a wind-tunnel, and then in a further series of experiments to investigate the related adjustments made by the cardiovascular system in meeting the increased tissue oxygen demand during flight. Some of the variables were also recorded from free-flying birds and compared with those obtained from pigeons in the tunnel in order to give an indication of the relation of the data obtained by the wind-tunnel technique to that occurring in nature.

MATERIALS AND METHODS

Flights in wind-tunnel

Five pigeons (*Columbia livia*), whose mass ranged between 0.39 and 0.48 kg, were trained to fly in a wire-mesh cage $1.22 \times 1.22 \times 1.22$ m which was placed in a boundary-layer wind-tunnel. One of the birds was a homing pigeon and the other four were white kings. The tunnel, which is housed in the Mechanical Engineering Department at the University of British Columbia, Vancouver, has a horizontal, 24 m long test section, which is 2.5 m wide and 2 m high. The wind speed was varied by changing the pitch of the fan which drew air into the tunnel from the room. Wind speed was routinely measured with a pitot tube, but the velocity profile and turbulence of the air inside the wire cage was measured with a DISA 55D01 constant-temperature

anemometer which was connected to a DISA linearizer (type 55D10) and a DISA R.M.S. voltmeter (type 55D35). This showed that in the central 0.6×0.6 m core of the cage, where the birds flew for the majority of the time, air flow was uniform and the mean turbulence intensity was $< 3\%$ at an air velocity of 10 m s^{-1} . During experiments an investigator was inside the wind-tunnel by the side of the cage and his presence increased wind velocity and absolute turbulence intensity by $< 10\%$. There was thus no change in relative turbulence intensity.

The birds were trained to fly by a method similar to that described by Tucker (1968). The floor of the cage was electrified and the birds' feet were soaked in saturated CaCl_2 to ensure good electrical contact with the grid. The bird was placed on a perch inside the cage with the tunnel turned on and wind speed at approximately 5 m s^{-1} . The perch was removed from the cage and placed back almost immediately. The bird fluttered for a very short while and landed back on the perch. Whenever the bird landed on the floor it received an instantaneous, mild electric shock and began to fly again. Attempts were made to train 12 birds but 7 of these showed no inclination to fly at all, despite the shock treatment. In fact it was soon clear which birds were and which were not going to respond to training at an early stage. With each trainable bird, the time for which the perch was removed and the wind speed were both gradually increased so that after about 2 weeks training the bird could fly at 10 m s^{-1} for 10 min or more. Thus, a flight was begun by removing the perch and ended by replacing the perch. The speed of 10 m s^{-1} was chosen as this is within the velocity range where oxygen uptake is minimal for the pigeon (Pennycuik, 1968). Early experiments showed that oxygen uptake and body temperature had settled to a steady level within 6 min, so a flight time of 10 min seemed adequate and all trainable birds managed to fly for this time without much difficulty, except after cannulation of their blood vessels (see later).

Deep body temperature (T_b) was measured by a Y.S.I. telethermometer probe which was placed into the rectum and the output from the thermometer was recorded on a Moseley potentiometric pen recorder (Hewlett Packard Ltd). Heart rate was measured by placing one subcutaneous electrode on top of the head and another at the base of the tail. Electromyograms from the pectoralis major muscles were obtained by placing subcutaneous electrodes either side of the sternum. In a number of flights respiratory frequency was obtained by an impedance technique. Subcutaneous electrodes were placed at the tip of the sternum and dorsal to this above the vertebral column and the electrodes were connected to a Biocom impedance converter (Model 991, Culver City, California). The reliability of this technique was tested in one bird by comparing the output of the impedance converter with that of a miniature thermocouple placed in the lumen of the trachea. The impedance technique was found to be quite satisfactory when the bird was at rest and during flight, but was sometimes less satisfactory at the end of a flight when the bird was panting. Heart rate, respiratory frequency and muscle E.M.G. were routinely recorded on a Techni-Rite recorder and, on a few occasions, respiration and muscle E.M.G. were recorded on a Brush 220 two-channel recorder.

Oxygen consumption and carbon dioxide production were measured by a method similar to that described by Tucker (1968). The bird wore a celluloid mask which covered the beak and nose but not the eyes. The mask was stitched to the bird by

three tabs and was of a loose fit. A flexible tygon tube (2.5 mm I.D. 1 mm wall thickness) entered the front of the mask and was attached by sutures to the bird's back (Fig. 1). Suction was applied to this tube so that air flowed into the mask and together with the expired gases was carried into the tube. A thermocouple was positioned at the entrance to the tube inside the mask so that respiratory frequency could be monitored. The mass of the mask and the tygon tube was 18 g.

A vacuum pump sucked air through the mask at approximately 2 l min⁻¹ when the bird was at rest and at between 9 and 10 l min⁻¹ during a flight. Both of these rates are substantially greater than the peak inspiratory flow rates measured by Hart & Roy (1966) in pigeons under similar conditions, and tests showed that transition from one flow rate to another had no effect upon the calculated values of \dot{V}_{O_2} or \dot{V}_{CO_2} when the wind-tunnel was turned off. However, when the tunnel was on and the wind speed was 10 m sec⁻¹, air had to be drawn through the mask at the higher rate of 9–10 l min⁻¹ in order to obtain stable, reliable recordings of \dot{V}_{O_2} and \dot{V}_{CO_2} . Thus, the higher flow rate was, in practice, used throughout the period that the wind-tunnel was on and because the tunnel could not be turned off quickly at the end of a flight, air was drawn through the \dot{V}_{O_2} mask at the higher rate after the pigeons had landed. As \dot{V}_{O_2} fell quickly to the pre-flight level after the pigeons had landed, the measurements of \dot{V}_{O_2} at this time were less accurate than those when the birds were resting or when they were flying. The gas was dried before passing through a flowmeter and the gas analysers. A separate pump pumped a fraction of the gas through a Beckman model F3 paramagnetic O₂ analyser and through a Beckman L/B infra-red CO₂ analyser model 15a. The output of the former was displayed on a Hewlett Packard 680 M strip chart recorder while that of the latter was displayed on a Bausch and Lomb VOM 7 potentiometric recorder. The gas analysers were calibrated with gas mixtures of accurately known composition and the lag of the system was of the order of 1 min. Carbon dioxide production and oxygen uptake were calculated by multiplying the flow rate of air coming from the mask by the difference in the concentration of the respiratory gas in air going into and leaving the mask. Unless R.Q. = 1, unequal amounts of the respiratory gases were exchanged. This means that the flow rate of air into the mask was different from the flow rate of air leaving the mask. This change in flow rate had a negligible effect on the calculation for \dot{V}_{CO_2} because of the low value of F_{I,CO_2} ; it could, however, have a large effect on the calculation for \dot{V}_{O_2} (depending on R.Q.). Oxygen uptake, calculated by the method described above, was corrected for R.Q. by the following formula:

$$\dot{V}_{O_2} \text{ (corrected)} = 1.265\dot{V}_{O_2} \text{ (calc)} - 0.265\dot{V}_{CO_2}.$$

All respiratory gas volumes have been corrected to S.T.P.D., and R.Q. was calculated from the mean values of \dot{V}_{O_2} and \dot{V}_{CO_2} .

A cannula (PE90; 0.6 mm I.D., 1 mm O.D.) was inserted into the left jugular vein and advanced until its tip came to lie in the right atrium. This was used for measuring venous blood pressure and for sampling mixed venous blood. Another cannula (PE 90) was inserted into the right sciatic artery and was used for measuring arterial blood pressure and for sampling arterial blood. These operative procedures were performed under local Xylocaine anaesthesia. Blood pressures were monitored by fluid-filled Hewlett Packard 267 BC differential pressure transducers and recorded on a Beckman



A pigeon flying in the cage in the wind-tunnel while wearing a \dot{V}_{O_2} mask. Note the sample tube and thermocouple lead from the mask positioned above the head and along the back of the animal.

two-channel dynograph. One side of each pressure transducer was connected to an open-ended, fluid-filled tube attached to the bird's back. This allowed instantaneous compensation in the zero level as the pigeon changed height during a flight. The length of each cannula was approximately 2 m.

Blood samples (0.3–0.5 ml) were taken anaerobically before and during a flight. The cannulae were filled with heparinized saline. Contamination of blood for analysis with saline was minimized by having two syringes connected by three-way taps connected to each cannula. The saline was removed from the cannula into one syringe and rejected. Blood was drawn into the same syringe and used to flush the dead space of the sample syringe which was eventually filled with the required volume of blood for analysis. Any remaining blood was injected back into the bird and the cannula was refilled with heparinized saline. The total amount of blood removed from any one bird did not exceed 2 ml. The fact that the haematocrit values of the pigeons in the present study are in close agreement with those reported by Bouverot, Hildwein & Oulhen (1976) indicates that plasma skimming or mixing of the blood with saline did not occur to any significant extent in the present experiments. Blood which was subsequently analysed did not stay in the cannula for longer than 1 min. Trials involving mixed venous blood stored in the cannula for 5 min with the wind velocity at 10 m s^{-1} , showed that blood sampled close to the bird had similar blood gas tensions to that sampled 2 m along the cannula. Thus, gas diffusion across the wall of the cannula was not a problem during the experiments. Gas tensions (P_{O_2} and P_{CO_2}) and pH were measured with a Radiometer acid/base analyser (PHM 71) and a blood micro system (BMS3, Mk 1) which housed the appropriate electrodes and thermostatically controlled their temperature at the body temperature recorded from the resting bird. The electrodes were calibrated with gas mixtures of accurately known composition or with precision buffers. Oxygen content of the blood was measured by a Lex- O_2 -Con oxygen content analyser (Lexington Instruments Ltd). Blood lactate was determined enzymically (see Sigma bulletin no. 826) some days after a $100 \mu\text{l}$ sample had been fixed with 8% perchloric acid and stored in a deep freeze. Assays were carried out on a Unicam SP 1800 dual-beam spectro-photometer. All blood samples, except arterial blood taken during a flight, were analysed immediately for their gas tensions, contents and pH. The arterial blood taken during a flight was stored for approximately 15 min in ice before it was analysed. Tests showed that such storage did not affect the measured variables. The values of blood P_{O_2} , P_{CO_2} and pH were corrected for the rise in body temperature of the birds during flight (cf. Holmgren & McIlroy, 1964).

All of the measured variables were monitored from the trained birds under four conditions, namely at rest on the perch with the wind-tunnel off and with no visual disturbance; on the perch with the wind-tunnel on; during a flight at 10 m s^{-1} for at least 7 min; and during recovery from the flight. Just before the flight started, one of the experimenters climbed into the wind-tunnel and positioned himself next to the cage, so that he could remove and replace the perch. During an initial series of flights, deep body temperature alone was measured. In another series, heart rate, respiratory frequency and muscle E.M.G. (wing-beat frequency) were monitored together. In a third series, oxygen uptake, carbon dioxide production and respiratory frequency were monitored by themselves and together with deep body temperature or heart rate. During the final series of flights, arterial and venous blood pressures, blood gas

tensions, blood gas contents and blood lactate were measured. All experiments were performed at a mean air temperature of 25.5°C and an average R.H. of 60%.

From the second and third series of flights it was found that the mask had no significant effect on heart rate during flight, but did cause a 4% increase in respiratory frequency and a 1°C rise in body temperature above the values recorded from birds flying without a mask. During the final series of flights, the birds had, 4 h before the flight, undergone some minor surgery, and under these conditions they were in a more excited state while at rest and tended to tire more quickly during flight in comparison with the other experimental series.

A separate series of experiments was performed on four different pigeons, whose mass was between 0.32 and 0.5 kg, to determine the effect of thermal polypnoea on blood gas tensions and oxygen uptake. The variables were measured, by similar techniques to those already outlined, in animals resting on a perch at normal body temperature and during polypnoea associated with an increase in deep body temperature of $2\text{--}3^{\circ}\text{C}$. The animals were heated by way of a heating thermode in the rectum, and/or by an infra-red lamp located above them. A flow of room air was maintained over the animal in order to keep the ambient temperature as low as possible. Thus it was hoped to simulate the conditions at the end of a flight in the tunnel with the body temperature of the animal elevated and with accompanying polypnoea.

Free-range flights

For comparison with the flights in the wind-tunnel, data were also obtained from pigeons during free-range flights using F.M. telemetry. The transmitter used was a Narco Bio-Systems Model E3 and it was held on to the back of the pigeon in a cotton 'saddle' by elastic loops passing around the wings. The transmitter, battery and leads had a combined mass of 11.4 g. The signal was received by twin Yagi antennae which were mounted at right angles to each other at the top of a pole 7 m high close to the pigeon coops. The receiver was an E & M 1100-5 single-channel system and the signal was transferred on to either a Techni-Rite or a Brush pen-recorder.

The position of the electrodes for recording E.C.G. and electromyograms of the pectoralis major muscles were as previously described for the flights in the wind-tunnel. Respiratory frequency was monitored by a thermistor with a 1 s time constant (Fenwal GC3 2J3) which was placed in the lumen of the trachea. All leads were passed subcutaneously, to the transmitter. Records were obtained from voluntary flights, the duration of which ranged from 4 to 37 s with the majority in the 12-14 s range.

Numerical data are given as means \pm S.E. of mean. Students *t* test was used to test the significance of any difference between two mean values and the word significant in the present report means significant at the 95% confidence level ($P < 0.05$).

RESULTS

Flights in wind-tunnel

Rest

After implantation of electrodes or cannulae etc., the birds were left for 2-4 h standing on the perch in the wind-tunnel free from visual disturbance and with the tunnel motor turned off. All of the variables were obtained under these conditions and

Table 1. *Mean values + S.E. of mean of respiratory and cardiovascular variables measured in pigeons at rest and after 6 min of steady, level flight at a speed of 10 m s⁻¹.*

(Resting values were obtained with the wind-tunnel turned off and with the tunnel on.

The number of observations, *n*, is given, with number of animals in parentheses.)

	Resting		Flying at 10 m s ⁻¹
	Tunnel off	Tunnel on	
Heart rate (min ⁻¹), <i>n</i> = 12 (5)	115 ± 2	222 ± 20	670 ± 14
Mean arterial pressure (mmHg), <i>n</i> = 4 (3)	142 ± 6	150 ± 5	147 ± 7
Mean venous pressure (mmHg), <i>n</i> = 4 (3)	1·2	—	2·5
Respiratory frequency (min ⁻¹), <i>n</i> = 16 (5)	19·7 ± 1·6	59·4 ± 15·9	411 ± 8·8
Oxygen uptake (ml kg ⁻¹ min ⁻¹ S.T.P.D.), <i>n</i> = 9 (3) (\dot{V}_{O_2})	20·3 ± 0·7	34·7 ± 2·3	200 ± 5·9
Carbon dioxide production (ml kg ⁻¹ min ⁻¹ S.T.P.D.), <i>n</i> = 9 (3) (\dot{V}_{CO_2})	17·2 ± 1·4	30·3 ± 2·8	184 ± 6·4
Respiratory quotient, <i>n</i> = 9 (3)	0·85	0·87	0·92
<i>P</i> _{a,O₂} (mmHg), <i>n</i> = 4 (3) (O ₂ tension of arterial blood)	87 ± 2	—	95 ± 1
<i>C</i> _{a,O₂} (vol %), <i>n</i> = 4 (3) (O ₂ content of arterial blood)	15·1 ± 1·5	—	13·7 ± 1·2
pH _a , <i>n</i> = 4 (3) (pH of arterial blood)	7·43 ± 0·02	—	7·36 ± 0·02
<i>P</i> _{r,O₂} (mmHg), <i>n</i> = 4 (3) (O ₂ tension of mixed venous blood)	57 ± 2	—	42 ± 5
<i>C</i> _{r,O₂} (vol. %), <i>n</i> = 4 (3) (O ₂ content of mixed venous blood)	10·5 ± 1·3	—	5·4 ± 0·6
pH _r , <i>n</i> = 4 (3) (pH of mixed venous blood)	7·36 ± 0·01	—	7·24 ± 0·03
<i>P</i> _{a,CO₂} (mmHg), <i>n</i> = 4 (3) (CO ₂ tension of arterial blood)	27 ± 0·6	—	16 ± 0·6
<i>P</i> _{r,CO₂} (mmHg), <i>n</i> = 4 (3) (CO ₂ tension of mixed venous blood)	35 ± 0·4	—	32 ± 2
Haematocrit (%), <i>n</i> = 4 (3)	42 ± 1·3	—	41 ± 1·5
Lactic acid (mg %), <i>n</i> = 4 (3)	9·0 ± 2·7	—	59·8 ± 21·4
Ambient temperature (°C)	25·5	25·5	25·5
Body temperature (°C), <i>n</i> = 5 (5)	41·3 ± 0·1	—	43·3 ± 0·2
Mass (kg), <i>n</i> = 5	0·442 ± 0·018	—	—

are given in Table 1 and Fig. 2. It is these which are taken as the resting values and with which the data obtained during flight are compared. Resting heart rate, respiratory frequency and oxygen uptake were lower than the values previously reported for the pigeon (Hart & Roy, 1966; Butler, 1970; Butler & Taylor, 1974) and the heart beat was often irregular (Fig. 3*a*). When the wind-tunnel was turned on the birds were disturbed. They had to work harder to stay on the perch; the noise level was high and eventually one of the investigators was in the tunnel with them. Figs. 3(*a*, *b*) show the increase in heart rate and respiratory frequency of one animal associated with the wind-tunnel being turned on and the mean effects on these and some of the other measured variables are given in Table 1 and Fig. 2. It can be seen that there were substantial increases in both \dot{V}_{O_2} and \dot{V}_{CO_2} , while R.Q. increased slightly from 0·85 to 0·89.

Blood samples were taken from the cannulated birds when the wind-tunnel was off. However, heart rate was not as low as that recorded during the earlier experiments, being 171 beats min⁻¹ on average (Table 1). The blood gas values were similar to those reported previously by Butler & Taylor (1974). As \dot{V}_{O_2} , $a - \bar{v}_{O_2}$ content difference and heart rate are known, it is possible to calculate cardiac output (\dot{Q}) and cardiac stroke volume. However, during the measurement of \dot{V}_{O_2} , the mean value for resting heart

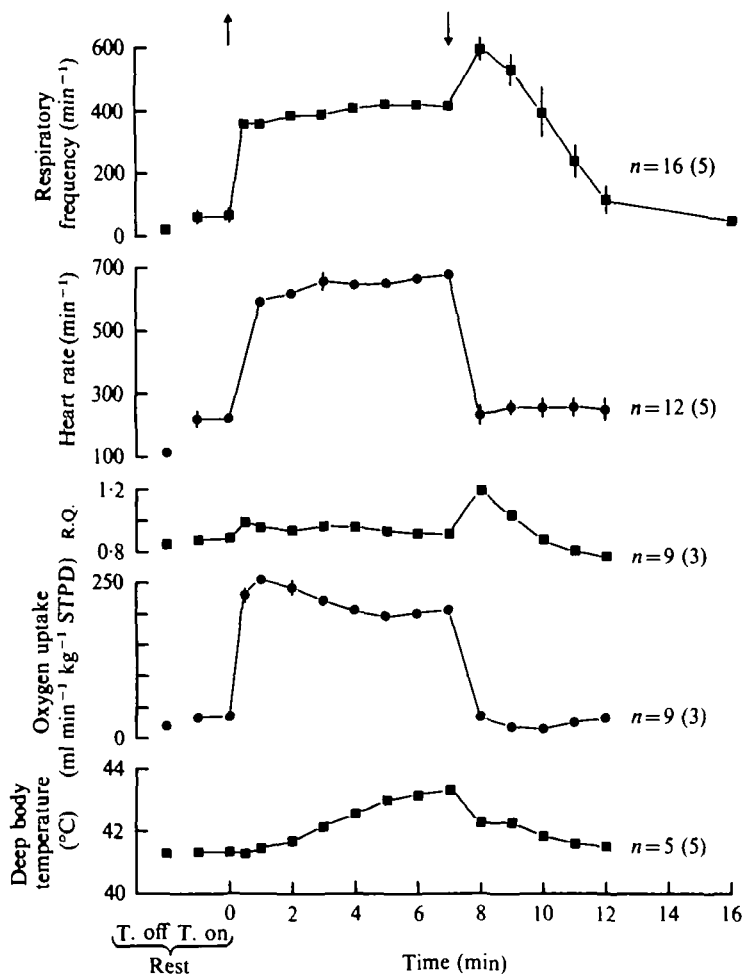


Fig. 2. Changes in respiratory frequency, heart rate, respiratory quotient (R.Q.), oxygen uptake and body temperature in pigeons before, during and after flying at 10 m s^{-1} for 7 min. Each point is the mean value of a number of observations (n) which is given close to each line. In parentheses, associated with each value of n , is the number of animals from which the observations were obtained. Vertical lines associated with each point are \pm s.e. of mean. Where vertical lines are absent, the s.e. of mean is within the limits of the symbol except for R.Q. which was computed from the mean value of \dot{V}_{O_2} and \dot{V}_{CO_2} and thus lacks a standard error. Arrows indicate points of take-off and landing. Resting values were taken when the tunnel was turned off (T. off) and when the tunnel was on (T. on).

rate, was $118 \text{ beats min}^{-1}$ (i.e. not significantly different from the resting value obtained without the \dot{V}_{O_2} mask on, see Table 1). As this heart rate is 70% of the value recorded when blood samples were taken, it is likely that the resting \dot{V}_{O_2} given in Table 1 is lower than it was at the time of sampling the blood. Butler (1970) recorded a \dot{V}_{O_2} of $25.5 \text{ ml kg}^{-1} \text{ min}^{-1}$ s.t.p.d. in pigeons with a heart rate of $171 \text{ beats min}^{-1}$. If this value is used to calculate resting cardiac output, then $\dot{Q} = 245 \text{ ml min}^{-1}$ ($555 \text{ ml kg}^{-1} \text{ min}^{-1}$). At a heart rate of $171 \text{ beats min}^{-1}$, stroke volume would be 1.44 ml . As the mean arterial blood pressure is also known, total peripheral resistance can be calculated. This was $4.62 \times 10^4 \text{ dyne s}^{-1} \text{ cm}^{-5}$.

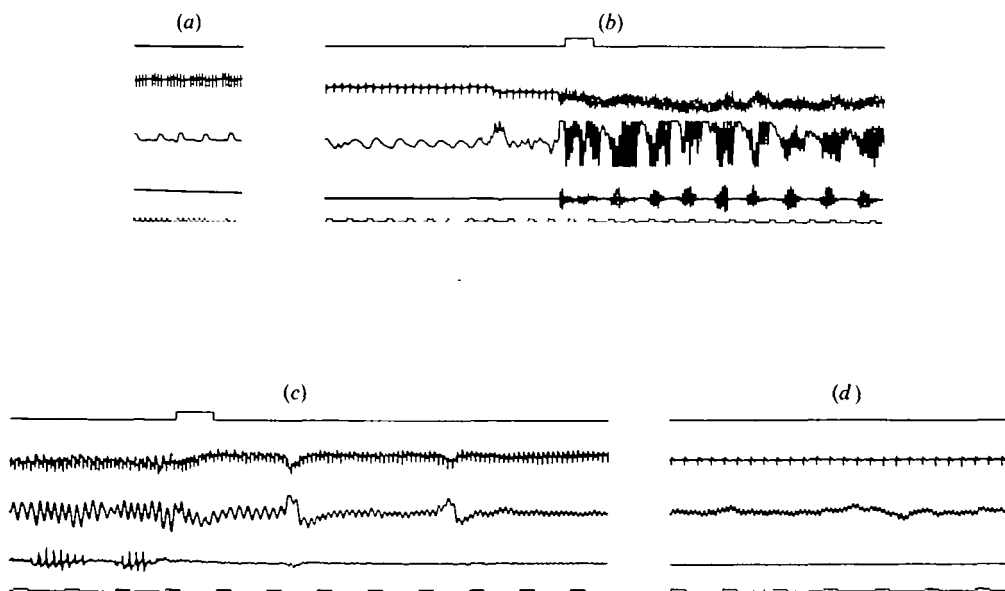


Fig. 3. Traces from a pigeon of mass 0.45 kg showing changes in heart rate, respiratory frequency and E.M.G. activity in pectoralis major muscles before, during and after flying at 10 m s^{-1} . (a) resting in wind-tunnel with the tunnel turned off, (b) take-off, (c) landing after flying for 10 min, (d) $2\frac{1}{2}$ min after landing. In each series, the traces from top to bottom are: event marker (up on trace indicates point of take-off or landing), E.C.G., respiratory movements recorded by impedance pneumograph (up on trace, inspiration), E.M.G. from pectoralis major muscles, time marker (s).

Flight

Immediately that the perch was removed and the bird began to fly, there were increases in heart rate and respiratory frequency (Fig. 3b) to $590 \pm 13 \text{ beats min}^{-1}$ and $355 \pm 18 \text{ breaths min}^{-1}$ respectively. Both of these variables continued to increase slowly so that after 7 min of level flight, heart rate was $677 \pm 9 \text{ beats min}^{-1}$ and respiratory frequency was $406 \pm 9 \text{ breaths min}^{-1}$. Although heart rate was fairly constant during flight, respiratory frequency was variable (Figs. 3, 4). This variability is related to the beating of the wings. The birds did not beat their wings continuously but in bursts (Figs. 3, 4), and respiratory frequency was the same as wing-beat frequency during these bursts of activity. However, between the bursts of wing beating, respiratory frequency varied. Towards the beginning of a flight it was often slower between bursts of wing beating (Fig. 4a), whereas towards the end of a flight it was often faster between bursts of wing beating (Fig. 4b). The E.M.G. activity from the pectoralis major muscles occurred during the transition from inspiratory to expiratory air flow as indicated by the thermocouple in the trachea. The duration of each group of wing beats ranged between 0.5 and 2.5 s and contained between 4 and 19 wing beats at a frequency of 7 Hz. The amplitude of the E.M.G. signals gradually increased and then decreased again during a group of wing beats (Figs. 3, 4). The overall amplitude of the E.M.G. signals was greatest at take-off, gradually declining until a steady level was reached 3–4 min later.

Deep body temperature (T_b) increased relatively rapidly during the first 4–5 min of

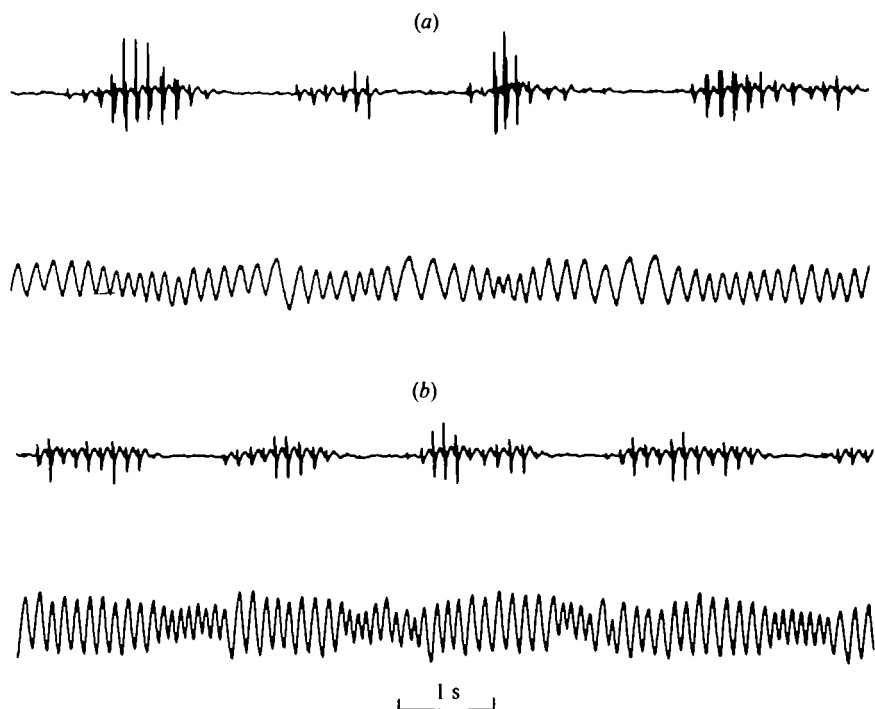


Fig. 4. Traces from a pigeon of mass 0.45 kg showing changes in respiratory frequency associated with periods of wing beating and with periods of gliding (a) at the beginning of a flight (1 min after take-off) when respiratory frequency decreased during the gliding period and (b) later in the flight (6 min after take-off) when respiratory frequency increased during the gliding period. In each series the traces from top to bottom are: E.M.G. from pectoralis major muscles, respiratory movements (up on trace, inspiration).

a flight, but from then on the rate of increase declined quite substantially (Fig. 2). On average, there was a 2°C increase in body temperature after 7 min of continuous flying in birds without the \dot{V}_{O_2} mask (Fig. 2, Table 1). Oxygen uptake and carbon dioxide production reached their highest values within 1 min of take-off when T_b was at its lowest, but they then declined as the flight progressed so that they were at their lowest flight values when T_b was at its highest (Figs. 2, 5). \dot{V}_{O_2} increased after take-off and after 1 min of flight it was, on average, $254 \pm 6 \text{ ml kg}^{-1} \text{ min}^{-1}$, but decreased to $200 \pm 6 \text{ ml kg}^{-1} \text{ min}^{-1}$ after 6 min of flying. The corresponding values for \dot{V}_{CO_2} were 248 ± 7 and $185 \pm 6 \text{ ml kg}^{-1} \text{ min}^{-1}$ respectively. R.Q. was 0.96 at 1 min after take-off, but fell slightly to 0.92, 6 min after take-off (Fig. 2, Table 1).

Despite the enormous rise in respiratory frequency and large fall in P_{a,CO_2} during flight, P_{a,O_2} rose slightly. The oxygen extraction by the tissues increased so that $a - \bar{v}_{O_2}$ content difference was $1.8 \times$ the resting value. Cardiac output was 1.07 l min^{-1} ($2.41 \text{ l kg}^{-1} \text{ min}^{-1}$), which is $4.37 \times$ the resting value. From the values of \dot{V}_{O_2} , \dot{Q} and heart rate, stroke volume was calculated as being 1.58 ml. The increase in \dot{Q} and $a - \bar{v}_{O_2}$ content difference do not of course account for the 10-fold rise in \dot{V}_{O_2} described above. This is because resting \dot{Q} was calculated from a value of \dot{V}_{O_2} which is higher than the resting value recorded in the present experiments (see earlier). Nevertheless these calculations do indicate the relative importance of changes in heart rate, stroke

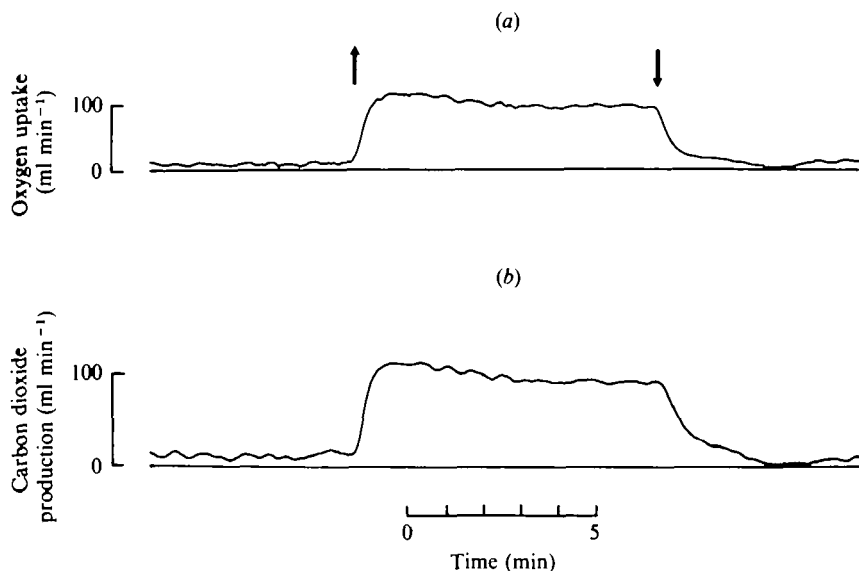


Fig. 5. Simultaneous recordings of (a) oxygen uptake and (b) carbon dioxide production of a pigeon of mass 0.48 kg before, during and after an 8 min flight at 10 m s^{-1} . Arrows indicate approximate points of take-off and landing, after allowing for the lag in the recording system. Note how both \dot{V}_{O_2} and \dot{V}_{CO_2} were at their highest levels 30 s after take-off and that gas exchange was close to zero approximately 3 min after landing.

volume and $a - \bar{v}_{O_2}$ content difference in their contributions to the raised \dot{V}_{O_2} during flight. As mean arterial blood pressure did not change during flight (Table 1, Fig. 6), total peripheral resistance (T.P.R.) fell by the same proportion as \dot{Q} increased. In fact T.P.R. after 6 min was $1.08 \times 10^4 \text{ dyne s}^{-1} \text{ cm}^{-5}$. Because of the movement of the blood pressure cannulae during flight, the output from the transducer monitoring venous pressure was electronically averaged. It can be seen from Fig. 6, however, that during bursts of wing beating there were large oscillations on the venous pressure trace. Despite the large ($6.5 \times$) increase in blood lactate during the flight, pHa fell slightly below its resting value. This was, no doubt, the result of a 40% reduction in P_{a,CO_2} .

The pattern of flight was similar for all of the birds, with the periods of wing beating taking them towards the front of the cage and the force of the wind taking them backwards between the bursts of wing beating. After 2–3 min of flying, all of the birds opened their mouth slightly and as the flight progressed the mouth was opened wider, although this was least obvious in the one homing pigeon.

Landing

Upon landing, heart rate, \dot{V}_{O_2} , \dot{V}_{CO_2} and Tb began to fall immediately (Figs. 2, 5), and within 2 min of landing heart rate, \dot{V}_{O_2} and \dot{V}_{CO_2} were not significantly different from the 'tunnel on' pre-flight values (Fig. 2). Respiratory frequency, however, increased upon landing (Figs. 2, 3) and this was undoubtedly related to the increased body temperature and thus served a thermoregulatory function. In fact, not only did the birds pant and gular flutter upon landing, but they also held their wings away from their bodies. The wind-tunnel was left on for about 5–10 min after the birds had landed and they clearly made use of the flow of air to assist in cooling their bodies.

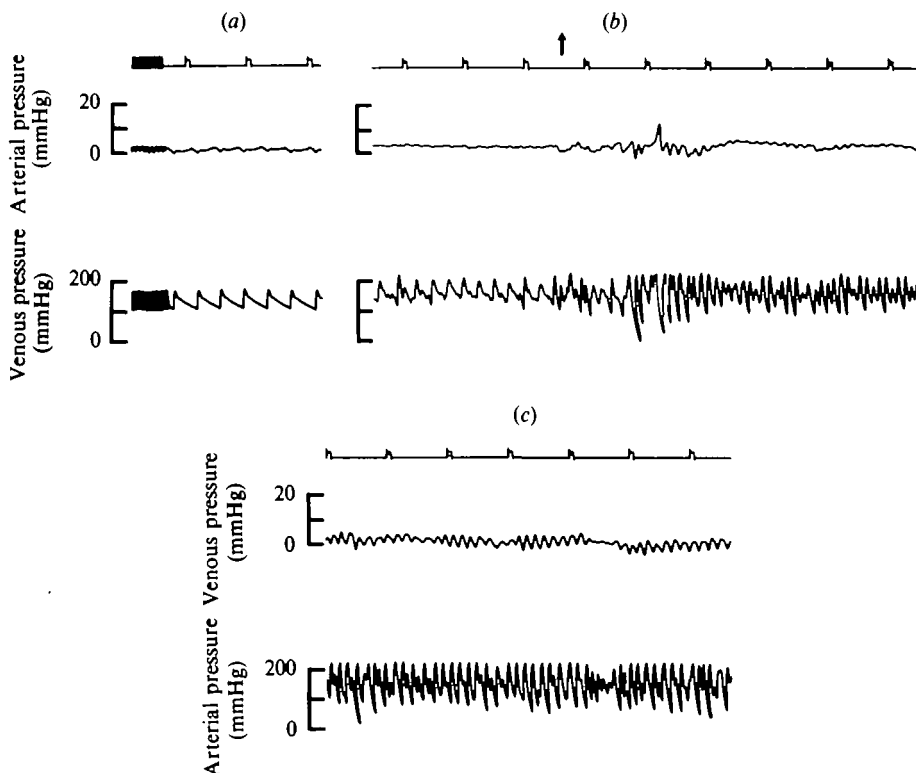


Fig. 6. Traces of arterial and venous blood pressures recorded from a pigeon of mass 0.48 kg before, and during a flight at 10 m s^{-1} (a) bird at rest with wind tunnel turned off, (b) take-off (arrow indicates point of take-off), (c) after 3 min of flight. In each series, traces from top to bottom are: time marker (s), venous pressure, arterial pressure. The venous pressure trace was electronically damped in (b) and (c).

On average, respiratory frequency was still above the 'tunnel on' pre-flight value 5 min after landing and its decline bore a close relationship to the reduction in \dot{V}_b (Fig. 2). However, in the homing pigeon, respiratory frequency returned to the 'tunnel on' pre-flight value within 3 min of landing. Respiratory quotient rose above 1 immediately after landing but had returned to the pre-flight value within 4 min of landing and then continued to fall below this value. No attempt was made to determine the magnitude of any oxygen debt after landing. This was in part related to the fact that it was not possible to turn the tunnel off immediately the bird landed and was thus not possible to draw air through the mask at the lower rate (see Materials and Methods). In view of the high accumulation of lactic acid during flight it was expected that \dot{V}_{O_2} would be above the pre-flight resting ('tunnel off') value for a short time after landing. It was most surprising therefore to find that \dot{V}_{O_2} was below this resting value for approximately 1 min at some time after landing (Fig. 5). The timing of this dip (2–4 min after landing) varied between birds and between flights for the same bird, so that it is not so obvious on the mean graph (Fig. 2), but it was a consistent feature of each flight and in some animals gas exchange almost ceased during this period (Fig. 5).

This feature was investigated further by simulating the post-flight conditions of

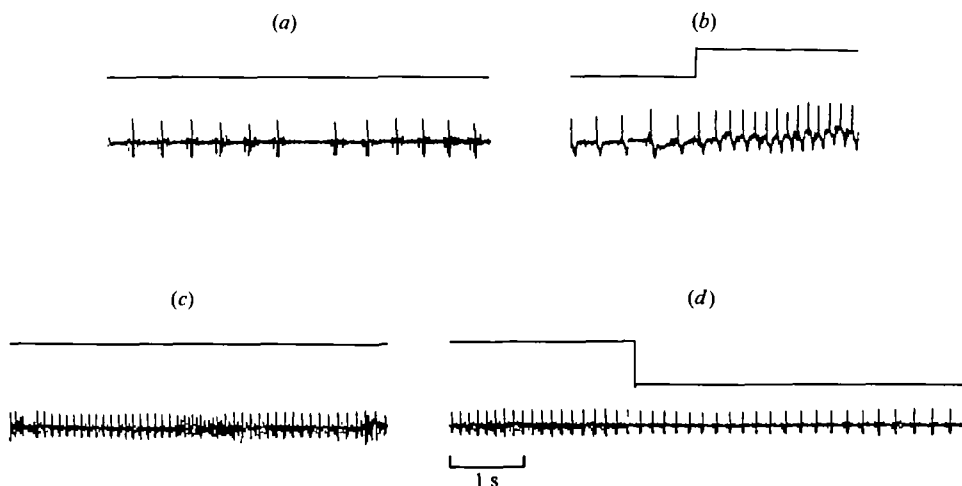


Fig. 7. Recordings of heart rate, using radiotelemetry, from a homing pigeon of mass 0.38 kg (a) bird at rest, (b) take-off (indicated by upward deflexion of event marker) for a spontaneous flight, (c) during a spontaneous flight, (d) landing (indicated by downward deflexion of event marker) after 15 s of natural flight.

high body temperature and normal ambient temperature. In the four birds investigated, body temperature was increased from an average value of 41.7°C to an average of 43.9°C . Because it always proved necessary to use the infra-red lamp as well as the thermode in order to get body temperature to the required level, ambient temperature also rose, on average from 25 to 32°C . Although respiratory frequency increased on average from 23 to $500\text{ breaths min}^{-1}$ there was no clear indication of any reduction in \dot{V}_{O_2} . In fact in two animals it remained the same and in one it increased. Only in one bird was there any sign of a reduction in \dot{V}_{O_2} , and this was after the heater had been switched off. In this animal, oxygen uptake fell gradually to 73% of its previous steady value and then increased again over a period of approximately 1 min . The same animal showed a dramatic reduction in $P_{\text{a,CO}_2}$ during thermal polypnoea, from 30 to 16 mmHg . Two of the birds showed smaller reductions than this (from 28 to 20 mmHg) and in the remaining bird there was no reduction in $P_{\text{a,CO}_2}$ at all during thermal panting.

Free-range flights

As when the birds were resting in the wind-tunnel, heart rate in the free-range birds was quite arrhythmic at rest (Figs. 3, 7). Immediately upon take-off, heart rate increased to $470\text{ beats min}^{-1}$ and after 15 s was approximately $600\text{ beats min}^{-1}$ (Figs. 7, 8b).

Pre-flight respiratory frequency was remarkably high compared with those birds in the wind-tunnel, but upon take-off it increased to an average of $475\text{ breaths min}^{-1}$. After 10 s of flying it was down to $375\text{ breaths min}^{-1}$ (Fig. 8a). Both homing pigeons and white kings were used in these free-range flights. Respiratory frequency was monitored from homers only, whereas heart rate was recorded from both types. There were no great differences in heart rate between the two types during the flights. Upon landing, however, heart rate recovered much more quickly in the homers than it did

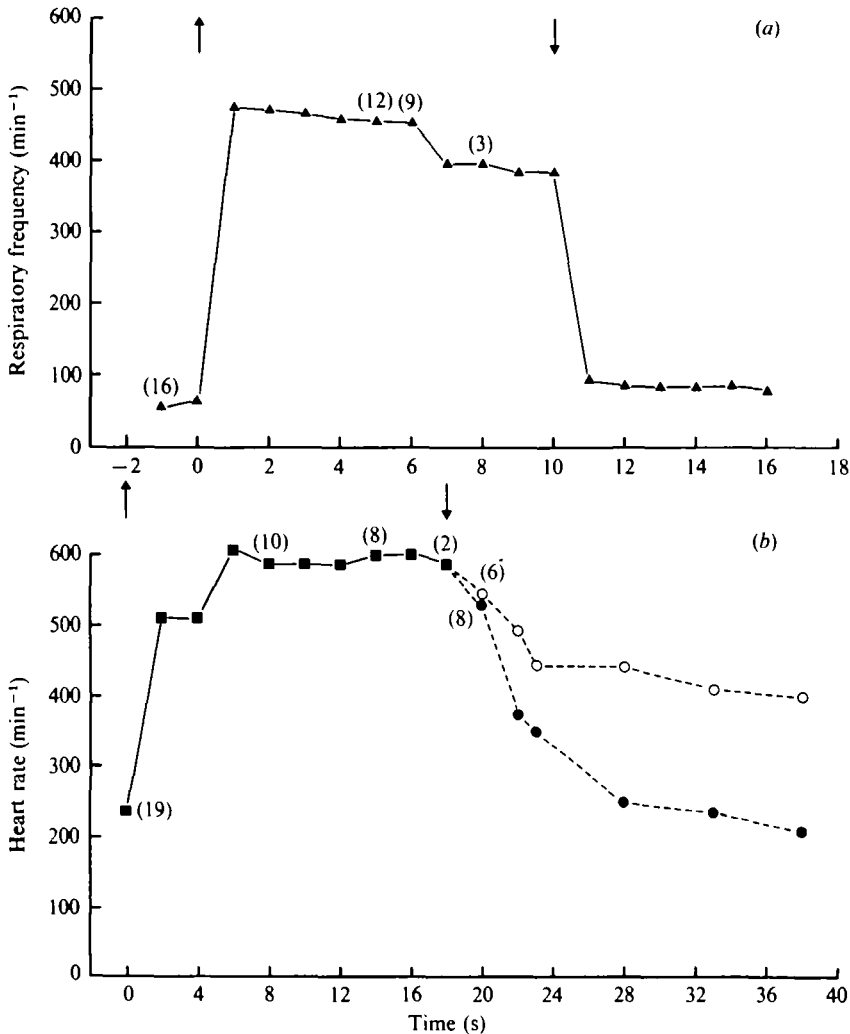


Fig. 8. Changes in (a) respiratory frequency and (b) heart rate in spontaneously flying pigeons. Each point is the mean value of a number of flights. This number is indicated next to some of the points. Respiratory frequency was obtained from homing pigeons alone, whereas heart rate was obtained from homers and white kings. In (b) the flight values from both white king pigeons and homing pigeons were pooled as there was no significant difference between the two types. As the heart rate of the homers recovered quicker than that of the white kings, there are two recovery lines, one (●) for the homers and the other (○) for the white kings. For each graph, the arrows indicate the points of take-off and landing.

in the whites (Fig. 8b). The changes in heart rate and respiratory frequency during voluntary flight were similar to those recorded by Hart & Roy (1966).

Perhaps the most revealing information from the free-flying birds is illustrated in Fig. 9. This shows the E.M.G. activity from the pectoralis major muscles during a spontaneous flight of 18 s duration. At take-off the pigeons in the tunnel flapped their wings in short (< 2 s) bursts of 5–7 flaps and the amplitude of the E.M.G. signals was somewhat larger than later during the flight. Upon landing, E.M.G. activity ceased as the bird settled back on the perch (Fig. 3c). At the beginning of a free-range flight on

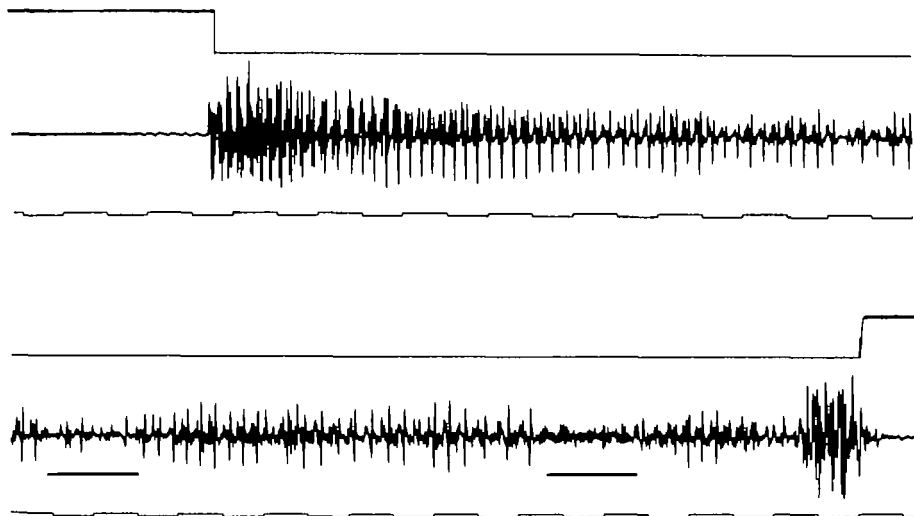


Fig. 9. Continuous record of the electromyogram from the pectoralis major muscles of a pigeon during a free, spontaneous flight of 18 s duration. The traces from top to bottom are: event marker (down on trace indicates point of take-off, up on trace indicates point of landing), E.M.G. from pectoralis major muscles, time marker (s). Note the large amplitude of the E.M.G. signal on take-off and landing, and its virtual absence during periods of gliding (indicated by bar under E.M.G. trace).

the other hand, the wings beat continuously as the bird gained altitude with the amplitude of the E.M.G. signal gradually decreasing as level flight was achieved. The flapping period during flight was longer than any of those measured from birds in the wind-tunnel and a large burst of muscle activity occurred at the end of the flight, presumably associated with the extra effort involved in decelerating and landing.

DISCUSSION

It is quite clear, by comparing the pattern of wing beating and the E.M.G. signals obtained from free-flying pigeons with those obtained from pigeons flying in a wind-tunnel, that the latter situation forced the bird to fly in an abnormal manner. Although in both situations the animal tended to alternate wing flapping with gliding, in the wind-tunnel the duration of the flapping period was shorter. This was imposed on the bird because the duration of these two periods was largely determined by the length of the cage and the wind speed. That this interference with normal flight behaviour had little effect on the other measured variables can, to some extent, be inferred from the fact that heart rate and respiratory frequency were similar during short free-range flights and the first 30 s of flight in the wind-tunnel. Also, recordings of deep body temperature from pigeons after free flights of more than 2 min (Hart & Roy, 1967) showed increases similar to those recorded from the maskless birds in the present investigation.

Tucker (1972) reported that metabolic rate of gulls during flight was increased by as much as 10% as a result of the drag caused by the mask and tube. The bird must also increase its power output by 2–3% to overcome the weight of the mask and its tube (Tucker, 1974). As it was not possible to test the effect of drag from mask, tube

and leads on metabolic rate in the present experiments, the uncorrected values of \dot{V}_{O_2} and \dot{V}_{CO_2} are given. In view of Tucker's findings, it can be assumed that the values for \dot{V}_{O_2} and \dot{V}_{CO_2} during the flight given in this report are at least 12% higher than they would have been in birds with no mask, tubes or leads attached to them.

A curious feature of metabolic rate during flight was the fact that both \dot{V}_{O_2} and \dot{V}_{CO_2} were 25% higher 1 min after take off than they were 3 min later. Certainly, the amplitude of the E.M.G. signals from the pectoralis major muscles was higher at the beginning of a flight than after 3–4 min of flying, indicating that as the flight progressed, fewer muscle fibres were involved with each wing beat. As the pattern of wing beating did appear to be different in pigeons flying in our wind-tunnel compared with free-flying birds, the higher metabolic rate at the beginning of the flight may reflect the efforts of the bird to obtain a flight rhythm that propelled it at a constant 10 m s⁻¹. The size of the cage did not allow for any real deviation from this speed. Whether or not the high initial metabolic rate is related to any other factors, such as the changes in the mechanical efficiency of the muscles as their temperature rises, or to changes in the level of circulating catecholamines, remains to be seen. Tucker (1972) reported a similar phenomenon in the laughing gull, where the high initial metabolic rate lasted for 15 min during which time the birds flew rather erratically. On the other hand, budgerigars fly steadily within 10 s of take-off and show no significant variations in metabolic rate during flight at a constant velocity (Tucker, 1968). It is clear therefore that flying in a wind-tunnel does not have exactly the same effect on different species.

The increase in R.Q. to almost unity during flight is at variance with the data of Tucker (1972) from the laughing gull, where R.Q. was 0.74 during flight, but is similar to the findings of Thomas (1975) for bats. This rise in R.Q. from the resting value may be the result of at least two factors. Parker & George (1975) concluded that at take-off or when undergoing sudden changes in direction, birds use the white 'fast twitch' fibres of the pectoralis major muscles which metabolize glycogen, and that during more sustained activity the red 'slow twitch' fibres are utilized. These fibres metabolize mainly fat. As R.Q. did fall slightly as the flight progressed and yet respiratory frequency continued to climb, a switch in metabolism during the flight away from carbohydrates is implicated. Removal of CO₂ by the respiratory system in excess of its metabolic production may also have contributed to the rise in R.Q. (Hill, Long & Lupton, 1924). Certainly P_{a,CO_2} fell dramatically during flight, whereas P_{a,O_2} rose slightly.

Using the formula of Lusk (1928) for the calorific value of oxygen, and if 1 W equals 0.86 kcal h⁻¹, then the average power input of the pigeons after 6 min flying was 30.5 W. From the recent model of Pennycuick (1975), which incorporates many of the modifications to his original model (Pennycuick, 1968) suggested by Tucker (1973), the calculated power input of a pigeon with a mass of 0.442 kg, a wing span of 72 cm and flying at 10 m s⁻¹, would be 37.2 W. This is 24% higher than the value actually measured. The energy cost of travel (see Tucker, 1970) by our pigeons after flying for 6 min was 1.65 kcal (or 6.9 kJ) kg⁻¹ km⁻¹. This value compares favourably with those obtained from other birds (Tucker (1972) on laughing gull; Bernstein, Thomas & Schmidt-Nielsen (1973) on fish crow). If 12% of this cost results from the drag and weight of the mask and tubes (see earlier), then the energy cost of transport by the pigeon was closer to that of the laughing gull than to that of the fish crow. The

fact that the energy cost of flight for our pigeons was so close to values reported for other birds flying in wind-tunnels at the same speeds indicates that if our wind-tunnel did impose unnatural restrictions on the birds, then either these restrictions had a negligible effect on the metabolic rate of the animals during flight, or the wind-tunnels used by the other workers imposed similar restrictions on their birds.

The rise in respiratory and cardiac frequencies at the beginning of exercise were as immediate and dramatic as in mammals (Krogh & Lindhard, 1913) and, as has been pointed out for mammals (Dejours, 1964; Robinson, 1974), these initial changes are so sudden that they must be initiated by the nervous system; probably by a combination of central and peripheral influences. A similar argument must apply to birds. The maintenance and often intensification of these changes may rely on other factors. Although P_{a,O_2} did not fall, nor did P_{a,CO_2} rise, there was a fall in pH during flight, and this is known to stimulate the arterial chemoreceptors in mammals (Hornbein & Roos, 1963); also a rise in body temperature may have had a stimulating effect on ventilation (see Cunningham, 1974).

Whatever their cause, the functional significance of these changes is obvious, namely to provide the necessary oxygen to the active flight muscles. In mammals, ventilation volume rises in proportion to oxygen uptake over the majority of the range of steady-state exercise intensities (Cunningham, 1974). Only during severe exercise does ventilation rise in excess of \dot{V}_{O_2} (Robinson, 1974). The $20\times$ rise in respiratory frequency is similar to that found by Hart & Roy (1966) in free-flying pigeons. These authors also found that tidal volume did not change appreciably from the resting value. If that were also the case in our birds, then a $10\times$ rise in \dot{V}_{O_2} would have been accompanied by a $20\times$ rise in ventilation volume. This could mean that the pigeons were undergoing what in mammals is described as severe exercise or it could mean, as Zeuthen (1941) postulated, that ventilation in the pigeon during flight is approximately twice as great as that required for metabolic needs alone, with the extra ventilation being concerned with increasing the percentage of heat lost by evaporation. Certainly, the accumulation of lactic acid during the last series of flights would indicate that the exercise during that series was severe; whether or not this was the case during the other three series is not at all certain. It is possible therefore that the high respiratory frequency during flight in the earlier series was related to evaporative heat loss, which certainly seems to rise during free flight (Hart & Roy, 1966). Taking the figures of Hart and Roy for the percentage of heat lost by evaporation in pigeons at rest (6.7%) and during flight (16.7%), it is possible to calculate the thermal conductance of our birds. At rest virtually all of the metabolic rate (3.05 W) was dissipated as heat, thus 2.85 W were lost by conduction and radiation. With a body temperature of 41.3 °C and an ambient temperature of 25.5 °C, thermal conductance was 0.18 W °C⁻¹. If the mechanical efficiency during flight was 0.23 (Pennycuik, 1975), then 23% of the total metabolic rate (30.5 W) was used to propel the bird through the air so that 23.5 W were dissipated as heat and of this, 19.6 W were lost by conductance and radiation. So, with a deep body temperature of 43.3 °C and an ambient temperature of 25.5 °C, thermal conductance was 1.1 W °C⁻¹; an increase of 6.1 times over the resting value. This is almost the same rise as Hart & Roy (1967) found for local heat flow over the breast muscles of the pigeon during flight.

Despite an increase in ventilation far in excess of metabolic requirements, P_{a,O_2}

increased only slightly during flight and the majority of the increase in supply of oxygen to the cells from the blood was achieved by a large (sixfold) rise in heart rate, with stroke volume showing little change and $a - \bar{v}_{O_2}$ content difference doubling. Despite the presence of a large amount of oxygen in the venous blood during flight there was a marked rise in blood lactate. This somewhat contradictory situation may indicate that an appreciable percentage of the increased output from the heart was perfusing the skin for thermoregulation (see above). It should be remembered, however, that the birds tired more quickly during the last series of flights (when they had been cannulated) than they did in the earlier series. It is quite possible that although they were flying at the same velocity as before, they were undergoing severe exercise and were, in fact, more exhausted at the end of the last series of flights. Therefore, all of the variables recorded during the last series of flights should only be used to indicate the general trends of the cardiovascular adjustments that were taking place in the earlier series of experiments.

The movement of the wings themselves may have assisted the respiratory and cardiac pumps. Respiratory frequency certainly had a 1:1 relationship with wing beat frequency, as has been reported previously for the pigeon (Tomlinson & McKinnon, 1957; Hart & Roy, 1966). From the E.M.G. recordings, the downstroke of the wings occurred at the transition from inspiration to expiration and not during expiration as might have been expected. This is also in agreement with the findings of Hart & Roy (1966). Although there appears to be co-ordination between cardiac contraction and contraction of the pectoralis muscles during flight in budgerigars and finches, with the pectoral muscles contracting during diastole thus greatly assisting diastolic filling (Aulie, 1971), such a relationship is not apparent in pigeons (Aulie, 1972). There were, however, marked oscillations on the venous pressure trace during flight, even though the frequency response of the pressure monitoring system had been reduced. As these oscillations had the same frequency (7 Hz) as wing-beat frequency, it can be assumed that they were caused by movement of the wings. However, it cannot necessarily be assumed that they represent oscillations in venous pressure. Both these oscillations and indeed those on the arterial trace may be artifacts which resulted from the rhythmic movements of the pressure cannulae as the wings beat. Nevertheless, contractions of the pectoral muscles would be expected to cause a large reduction in their blood volume and thus aid venous return to some extent.

Upon landing, the two major changes that occurred during flight, namely hyperthermia and the development of an oxygen debt, had to be returned to normal. From the changes in heart rate and \dot{V}_{O_2} , it would appear that the immediate or alactacid component of the oxygen debt (Margaria, Edwards & Dill, 1933; Knuttgen, 1970) was repaid within 2 min of landing. However, the expected gradual decline in \dot{V}_{O_2} to a steady level over the next few minutes was interrupted by a distinct reduction in gas exchange. Although a similar reduction in \dot{V}_{O_2} during thermal panting has been reported for the Dik Dik (Hoppe *et al.* 1975), the only explanation that we have for this from our own attempts to simulate the conditions at the end of a flight and from the results of Calder & Schmidt-Nielsen (1966) on thermal polypnoea in pigeons, is that the hyperventilation that occurred upon landing reduced P_{a,CO_2} further (i.e. below the flight level) and that as a result of this, a slight depression of pulmonary ventilation occurred until P_{a,CO_2} was restored. Certainly, upon landing, R.Q. rose above unity, indicating that

CO₂ was being removed from the body in excess of metabolic production (Hill *et al.* 1924). As body temperature fell, so respiratory frequency declined, \dot{V}_{O_2} began to increase and R.Q. began to fall below the pre-flight resting level. This may indicate that as the slower, lactic acid component of the oxygen debt was being repaid, CO₂ was retained to maintain acid-base balance as lactic acid was removed (Hill *et al.* 1924).

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REFERENCES

- AULIE, A. (1971). Co-ordination between the activity of the heart and the flight muscles during flight in small birds. *Comp. biochem. Physiol.* **38A**, 91-97.
- AULIE, A. (1972). Co-ordination between the activity of the heart and the pectoral muscles during flight in the pigeon. *Comp. biochem. Physiol.* **41A**, 43-48.
- BERNSTEIN, M. H., THOMAS, S. P. & SCHMIDT-NIELSEN, K. (1973). Power input during flight of the fish crow, *Corvus ossifragus*. *J. exp. Biol.* **58**, 401-410.
- BOUVEROT, P., HILDWEIN, G. & OULHEN, P. L. (1976). Ventilatory and circulatory O₂ convection at 4000 m in pigeon at neutral or cold temperature. *Resp. Physiol.* **28**, 371-385.
- BUTLER, P. J. (1970). The effect of progressive hypoxia on the respiratory and cardiovascular systems of the pigeon and duck. *J. Physiol., Lond.* **201**, 527-538.
- BUTLER, P. J. & TAYLOR, E. W. (1974). Responses of the respiratory and cardiovascular systems of chickens and pigeons to changes in P_{a,O_2} and P_{a,CO_2} . *Resp. Physiol.* **21**, 351-363.
- CALDER, W. A. & SCHMIDT-NIELSEN, K. (1966). Evaporative cooling and respiratory alkalosis in the pigeon. *Proc. natn. Acad. Sci. U.S.A.* **55**, 750-756.
- CUNNINGHAM, D. J. C. (1974). Integrative aspects of the regulation of breathing: a personal view. In *MTP International Review of Science Physiology*, series 1. Vol. 2. *Respiratory Physiology* (ed. J. G. Widdicombe), pp. 303-369. London: Butterworth.
- DEJOURS, P. (1964). Control of breathing in muscular exercise. In *Handbook of Physiology*. Section 3. *Respiration*, vol. 1 (ed. W. O. Fenn and H. Rahn), pp. 631-648. Washington, D.C.: American Physiological Society.
- ELIASSEN, E. (1963). Preliminary results from a new method of investigating the physiology of birds during flight. *Ibis* **105**, 234-237.
- HART, J. S. & ROY, O. Z. (1966). Respiratory and cardiac responses to flight in pigeons. *Physiol. Zool.* **39**, 291-306.
- HART, J. S. & ROY, O. Z. (1967). Temperature regulation during flight in pigeons. *Am. J. Physiol.* **213**, 1311-1316.
- HILL, A. V., LONG, C. N. H. & LUPTON, H. (1924). Muscular exercise, lactic acid and the supply and utilization of oxygen. III. Lactic acid in blood and the respiratory quotient. *Proc. R. Soc. B* **96**, 455-475.
- HOLMGREN, A. & McILROY, M. B. (1964). Effect of temperature on arterial blood gas tensions and pH during exercise. *J. appl. Physiol.* **19**, 243-245.
- HOPPE, P. P., JOHANSEN, K., MALOIY, G. M. O. & MUSEWE, V. (1975). Thermal panting reduces oxygen uptake in the Dik Dik *Rhyncotragus kirkii*. *Acta physiol. scand.* **95**, 9A.
- HORNBEIN, T. F. & ROOS, A. (1963). Specificity of H ion concentration as a carotid chemoreceptor stimulus. *J. appl. Physiol.* **18**, 580-584.
- KNUTTGEN, H. G. (1970). Oxygen debt after submaximal physical exercise. *J. appl. Physiol.* **29**, 651-657.
- KROGH, A. & LINDHARD, J. (1913). The regulation of respiration and circulation during the initial stages of muscular work. *J. Physiol., Lond.* **47**, 112-136.
- LEFEBVRE, E. A. (1964). The use of D₂O¹⁸ for measuring energy metabolism in *Columbia livia* at rest and in flight. *Auk* **81**, 403-416.
- LINNARSSON, D. (1974). Dynamics of pulmonary gas exchange and heart rate changes at start and end of exercise. *Acta physiol. scand.*, Suppl., **415**, 1-68.
- LUSK, G. (1928). *The elements of the Science of Nutrition*, 4th edn. Philadelphia: W. B. Saunders.
- MARGARIA, R., EDWARDS, H. T. & DILL, D. B. (1933). The possible mechanisms of contracting and paying the oxygen debt and the role of lactic acid in muscular contraction. *Am. J. Physiol.* **106**, 689-715.
- MARGARIA, R., CERRETELLI, P., AGHEMO, P. & SASSI, G. (1963). Energy cost of running. *J. appl. Physiol.* **18**, 367-370.
- PARKER, G. H. & GEORGE, J. C. (1975). Effects of short and long term exercise on intracellular glycogen and fat in pigeon pectoralis. *Jap. J. Physiol.* **25**, 175-184.

- PENNYCUICK, C. J. (1968). Power requirements for horizontal flight in the pigeon *Columbia livia*. *J. exp. Biol.* **49**, 527-555.
- PENNYCUICK, C. J. (1975). Mechanics of flight. In *Avian Biology*, vol. v (ed. D. S. Farner and J. R. King), pp. 1-75. New York, London: Academic Press.
- ROBINSON, S. (1974). Physiology of muscular exercise. In *Medical Physiology*, 13th edn. (ed. V. B. Mountcastle), pp. 1273-1304. St Louis: Mosby.
- ROWELL, L. B. (1974). Human cardiovascular adjustments to exercise and thermal stress. *Physiol. Rev.* **54**, 75-159.
- THOMAS, S. P. (1975). Metabolism during flight in two species of bats. *Phyllostomus hastatus* and *Pteropus gouldii*. *J. exp. Biol.* **63**, 273-293.
- TOMLINSON, J. T. & MCKINNON, R. S. (1957). Pigeon wing-beats synchronized with breathing. *Condor* **59**, 401.
- TUCKER, V. A. (1966). Oxygen consumption of a flying bird. *Science, N. Y.* **154**, 150-151.
- TUCKER, V. A. (1968). Respiratory exchange and evaporative water loss in the flying budgerigar. *J. exp. Biol.* **48**, 67-87.
- TUCKER, V. A. (1970). Energetic cost of locomotion in animals. *Comp. biochem. Physiol.* **34**, 841-846.
- TUCKER, V. A. (1972). Metabolism during flight in the laughing gull, *Larus atricilla*. *Am. J. Physiol.* **22**, 237-245.
- TUCKER, V. A. (1973). Bird metabolism during flight: evaluation of a theory. *J. exp. Biol.* **58**, 689-709.
- TUCKER, V. A. (1974). Energetics of natural avian flight. In *Avian Energetics* (ed. R. A. Paynter), pp. 298-333. Cambridge, Mass.: Nuttall Ornithological Club.
- TUCKER, V. A. (1975). Flight energetics. *Symp. zool. Soc. Lond.* **35**, 49-63.
- TUCKER, V. A. & SCHMIDT-KOENIG, K. (1971). Flight speeds in birds in relation to energetics and wind directions. *Auk* **88**, 97-107.
- ZEUTHEN, E. (1942). The ventilation of the respiratory tract in birds. II. Respiration and heat regulation in the bird at rest at high temperature and in the flying bird. *K. Danske. Vidensk. Selskab., Biol. Medd.* **17**, 41-51.