

## RESPIRATORY PHYSIOLOGY OF HOUSE SPARROWS IN RELATION TO HIGH-ALTITUDE FLIGHT

BY VANCE A. TUCKER

*Department of Zoology, Duke University, Durham, North Carolina*

(Received 26 June 1967)

### INTRODUCTION

Some birds perform flapping flight at remarkably high altitudes. A commercial aircraft flying at 6400 m. (21,000 ft.) was struck by an object, evidently a mallard duck from the feathers recovered later from a dent in the aircraft (Manville, 1963). Radar echoes attributed to passeriform and charadriform birds have been regularly detected at altitudes of 6100 m. (20,000 ft.) or more during night migrations, although most birds migrate at altitudes below 1800 m. (6000 ft.) (Lack, 1960; Nisbet, 1963). There are reports of birds flying at 6100 m. or more in mountains (Aymar, 1935; Meinertzhagen, 1955). Hunt (1954), describing the 1953 British expedition to Everest, mentions that birds were observed flying at altitudes above 7940 m. (26,000 ft.).

Because of the properties of the atmosphere at 6100 m. and above, and human responses to these altitudes, it is difficult to understand how birds could fly at such altitudes. The atmospheric pressure at 6100 m. is 349 mm. Hg (Spector, 1956) with a partial pressure of oxygen ( $P_{O_2}$ ) of 73 mm. Hg. These values are less than half those at sea level. Bird flight at sea level probably requires a rate of oxygen consumption 8 or more times that at rest (Lasiewski, 1963; Le Febvre, 1964; Tucker 1968). In humans, such an increase in oxygen consumption represents heavy work. Resting unacclimated men at 6100 m. are in a state of incipient hypoxic collapse after 10 min. (Armstrong, 1952), and men acclimated to this altitude can sustain oxygen consumption at 8 times the basal level for only 5 min. (Pugh, 1958). Coma and death occur in unacclimatized men exposed to 7000 m. (23,000 ft.) (Luft, 1965). How then, can birds perform the strenuous activity of flapping flight at these altitudes?

In this paper I have examined some of the physiological problems of high-altitude avian flight by investigating oxygen consumption and oxygen transport by the circulatory system in resting house sparrows (*Passer domesticus*) exposed to a simulated altitude of 6100 m. and a temperature of 5° C. Although the sparrows under these conditions used less oxygen than during flight, oxygen consumption was more than twice the basal level. Also included are comparative data for white mice (*Mus musculus*) and observations on house sparrows and budgerigars (*Melopsittacus undulatus*) flying with and without supplemental oxygen at simulated high altitudes in a hypobaric chamber.

\* Supported by grants from the Duke University Council on Research (no. 840926) and the National Science Foundation (no. GB 3350). Mrs Marsha Poirier provided technical assistance. F. G. Hall provided the hypobaric chamber.

## METHODS

*Oxygen consumption, heart rate, respiratory rate and body temperature*

Sparrows were trapped outside the laboratory in May and June. Birds used for heart-rate measurements were kept on an inverted 12 hr. light-dark cycle for 6 days prior to use, and measurements were made during the dark cycle. These birds were freely supplied with water and game-bird food. Birds used in other experiments were trapped and used immediately. White mice of unspecified stock were obtained commercially.

Oxygen consumption was determined by placing a sparrow or a mouse in a 1 l. glass jar sealed with a rubber stopper. A sealed, diaphragm pump drew air at 600 ml./min. sequentially through a flowmeter, a needle valve and the jar. The air leaving the pump then passed through a second needle valve before continuing through Drierite to a recording Beckman paramagnetic oxygen analyser. The oxygen analyser was switched periodically to record the oxygen content of the air entering the jar. The pressure in the jar was regulated to within 1 mm. Hg of the desired level by manipulating the needle valves and referring to a mercury manometer. The jar was placed in a dark cabinet that maintained the temperature inside the jar at  $5 \pm 0.5^\circ \text{C}$ .

Oxygen consumption was calculated from the flow rate and oxygen analyser readings assuming a respiratory quotient (R.Q.) of 1. If the R.Q. actually were 0.7, the calculated values of oxygen consumption would be 6% too low (Depocas & Hart, 1957), but an error of this size is insignificant in the present study. All values for oxygen consumption refer to dry gas at  $0^\circ \text{C}$ . and 760 mm.

Heart rate could be measured simultaneously with oxygen consumption. Two electrocardiograph leads of flexible wire entered the respirometer jar through air-tight connections, and small safety pins with heads removed were soldered to the ends of the leads. The safety pins were compressed with forceps and released to grip firmly inside the flanges of 9 mm. wound clips. The wound clips were attached to the animal just prior to making measurements. For sparrows, one clip was placed in the axillary region, the other on the abdominal axillary region. For mice, one wound clip was placed over each shoulder blade. Heart rates were determined from an oscilloscope or an oscillograph recording.

Cloacal temperatures were measured to the nearest  $0.1^\circ \text{C}$ . with a polyethylene sheathed 30-gauge thermocouple inserted to a depth of 2 cm., or with a Schultheis quickreading thermometer.

Respirations were observed and timed with a stopwatch.

An animal was placed in the jar, and its oxygen consumption at sea level (760 mm.) was recorded for 2-3 hr. Its body temperature was then measured. The animal was returned to the jar, the pressure was reduced to 481 mm. (about 3700 m. or 12,000 ft.) and oxygen consumption was recorded for  $\frac{1}{2}$  hr. Finally, the pressure was reduced to 344 mm. (about 6100 m.), oxygen consumption was recorded for at least 1 hr. and then body temperature was measured. This procedure was carried out with five sparrows (mean weight, 22.5 g.) and five mice (mean weight, 36.4 g.).

In other experiments both oxygen consumption and heart rate were measured. For sparrows, the procedure was similar to that in the preceding paragraph except that body temperatures were not measured, and the birds were taken from sea level

directly to an altitude of 6100 m. within 3 min. Heart rates of mice could not be counted at sea level because of interference of muscle potentials. Consequently, mice were exposed to 6100 m. within 3 min. after being placed in the jar. At this altitude they became lethargic, and heart rates were easy to determine.

*Oxygen-dissociation curves, pH and  $P_{CO_2}$  of blood*

Ten oxygen-dissociation curves, each for an individual bird, were determined by the method of Tucker (1967) on whole, heparinized blood at 41° C. collected after decapitation. Blood from five of the birds was equilibrated with a partial pressure of carbon dioxide ( $P_{CO_2}$ ) of 10 mm. Blood from the other birds was equilibrated at a  $P_{CO_2}$  of 39 mm. Percentage saturation of the blood with oxygen ( $Y$ ) was calculated from the relation  $Y = 100 \times \text{oxygen content}/\text{oxygen capacity}$ . Oxygen content includes both dissolved oxygen and oxygen bound by haemoglobin. Oxygen capacity is the oxygen content of blood equilibrated with a  $P_{O_2}$  of 138 mm. at 41.0° C. Each oxygen dissociation curve was plotted as  $\log [Y/(100 - Y)]$  against  $\log P_{O_2}$ , since use of these co-ordinates simplifies identification of the  $P_{O_2}$  where half-saturation occurs ( $p_{50}$ ) and permits the curves to be shifted easily to different temperature and pH values (Brown & Hill, 1923).

Blood pH was determined on 10  $\mu$ l. samples with a Metrohm capillary electrode connected to a Beckman research pH meter. All pH values were determined at 41.0° C. Absolute and relative accuracy were  $\pm 0.01$  and  $\pm 0.002$  pH units respectively. The pH of each oxygen dissociation curve was taken as the mean of pH's measured at 100% saturation, and approximately 50% and 5% saturation. The Bohr effect was investigated by plotting  $p_{50}$  against the pH of the curve.

Oxygen dissociation curves adjusted to desired temperature and pH values were constructed in the following manner. Curves for eight blood samples were determined at pH values within 0.20 units of the mean *in vivo* blood pH (7.502) of birds at sea level. These curves were corrected to pH 7.502 by translating them along the  $\log P_{O_2}$  axis by an amount calculated from the relation describing the Bohr effect. Then  $\log P_{O_2}$  values were averaged at  $\log [Y/(100 - Y)]$  values of  $-1.00$ ,  $-0.50$ ,  $0.00$  and  $0.50$ , and a mean curve was constructed from these averages. This mean curve was translated along the  $\log P_{O_2}$  axis to obtain curves at other pH and temperature values. The temperature correction factor ( $\Delta p_{50}/\Delta^\circ \text{C.} = 1.35$ ) was determined from data on pigeon blood (Prosser, 1950).

The pH and  $P_{CO_2}$  of blood *in vivo* were determined by the method of Astrup (1956). A sparrow was decapitated over a beaker containing heparin, and the pH electrode was filled with blood from the bottom of the pool in the beaker within 5 sec. Experiments in which blood was squirted from a syringe into the beaker showed that blood pH did not change in this time. The remaining blood was divided into 2 parts and equilibrated at a temperature of 41° C. with air-CO<sub>2</sub> mixtures having  $P_{CO_2}$ 's of 10 and 39 mm. pH was measured in duplicate at each  $P_{CO_2}$ 's, and *in vivo*  $P_{CO_2}$  was determined by interpolation. To correct for the increased activity of blood with oxygenation, the following assumptions were made: the blood obtained from birds at sea level and 6100 m. was 85 and 20% saturated with oxygen, respectively, and the pH of blood changed 0.005 pH units for each gram of unsaturated haemoglobin per 100 ml. blood (Astrup, 1958).

*In vivo* pH and  $P_{\text{CO}_2}$  of blood were determined when sparrows were breathing air at normal atmospheric pressure or were breathing a mixture of nitrogen and air with a  $P_{\text{CO}_2}$  of 70 mm. equivalent to the  $P_{\text{O}_2}$  at about 6100 m. The bird was placed at 5° C. in an air-tight cylindrical plastic bag 25 cm. long and 5 cm. in diameter. Air or a mixture of nitrogen and air flowed in one end of the bag and out the other at a rate of 1000 ml./min. The inlet and outlet to the bag were through glass tubes 6 mm. in diameter and 7 cm. long. Blood samples were obtained without disturbing the gas mixture being breathed by the bird by cutting through the bag and decapitating the bird. The bird was placed in the bag 1 hr before its blood was sampled. No more than 3 sec. elapsed between the time the bird was picked up and the blood sample collected.

Plasma bicarbonate concentrations were calculated using a  $pK'$  of 6.07 (Severinghaus, Stupfel & Bradley, 1956*b*) and solubility factors for  $\text{CO}_2$  from Severinghaus *et al.* (1956*a*).

Haematocrit was determined by centrifuging  $1 \times 75$  mm. capillary tubes filled with blood at 19,000 g. for 5 min.

#### *Flight at high altitudes*

The ability of birds to fly at simulated high altitudes was investigated using two budgerigars trained to fly at approximately 40 km./hr. in a wind tunnel in a hypobaric chamber. One of the birds was trained to fly with a mask through which 2 l./min. of oxygen were flowing. Details of the wind tunnel and mask are described elsewhere (Tucker, 1968). In addition, house sparrows were observed following their release in the hypobaric chamber. There was a flight path approximately 2.5 m. long from one end of the chamber to the other.

#### *Heart and lung weights*

Heart and lung weights were measured for both sparrows and mice. Each organ was removed from the freshly killed animal, trimmed of large blood vessels and connective tissue, emptied of blood, blotted on tissue paper and weighed on an analytical balance.

### RESULTS

#### *Behaviour, oxygen consumption, heart rate, respiratory rate and body temperature*

Sparrows at sea level in the respirometer chamber were alert, and rested with their feathers fluffed, vigorously tried to escape from the chamber or searched through the sawdust at the bottom of the chamber. Mean values for oxygen consumption, heart rate, body temperature and respiratory rate are shown in Table 1.

At an altitude of 6100 m. there was no visible change in the behaviour of the birds. They were as alert and active as at sea level. However, mean oxygen consumption, heart rate and respiratory rate increased while mean body temperature decreased almost 2° C. (Table 1). Oxygen consumption was 2.2 times the nocturnal, basal rate of sparrows at sea level (calculated from King & Farner, 1960).

The response of mice to high altitudes was markedly different from that of the sparrows. At sea level the mice were continuously active, exploring the chamber, gnawing on the inlet and exhaust ports and digging in the sawdust. At 3700 m., the mice were lethargic and walked slowly around the chamber if they moved at all. At 6100 m.

they were comatose, although they responded to tapping on the chamber. They lay on their bellies and usually did not move although they could crawl slowly. Their mean body temperatures dropped 10° C. during the experiment, partly explaining their lethargic condition. Oxygen consumption at 6100 m. was only 46% of that at sea level (Table 1).

Table 1. *Physiological properties of house sparrows at 5° C. at sea level and at an altitude of 6100 m. Some data for laboratory mice are included. Each entry is a mean value, followed in most cases by a standard deviation and in parentheses, the number of observations*

	Sea level	6100 m.
Total atmospheric pressure (mm. Hg)	760	344
Body temperature (° C.)		
Sparrows	41·2, 1·3 (5)	39·4, 2·0 (5)
Mice	37·4, 0·8 (3)	27·3, 2·1 (5)
Heart rate (beats/min.)		
Sparrows	649, 136 (5)	722, 62 (5)
Mice	—	411, 100 (5)
	Respiration	
O <sub>2</sub> consumption, ml. (g. hr.) <sup>-1</sup>		
Sparrows	4·52, 0·45 (5)	5·54, 0·73 (5)
Mice	6·12, 0·39 (5)	2·80, 0·26 (5)
Respiratory rate (breaths/min.)	81, 20 (4)	112, 12 (4)
Effective ventilation, ml. (g. hr.) <sup>-1</sup>		
Actual volume	80·3	142
STP dry volume	64·3	47·3
Effective tidal volume, ml. (g. breath) <sup>-1</sup>	0·0165	0·0211
P <sub>A</sub> O <sub>2</sub> (mm. Hg)	100	28
P <sub>A</sub> CO <sub>2</sub> (mm. Hg)	39·5	27·2
Oxygen utilization, % (see text)	7	12
	Mixed venous and arterial blood	
O <sub>2</sub> capacity, ml. O <sub>2</sub> /100 ml. blood	19·1, 1·8 (23)	—
Haematocrit	48·8, 3·8 (22)	—
pH	7·502, 0·051 (5)	7·604, 0·027 (5)
pCO <sub>2</sub> (mm. Hg)	42·5, 0·8 (5)	30·2, 0·9 (5)
Plasma bicarbonate (mm./l.)	31·6, 5·4 (5)	25·1, 3·5 (7)
Buffer value, Δ[HCO <sub>3</sub> <sup>-</sup> ]/ΔpH	22·1, 1·5 (5)	21·1, 3·1 (7)
	Morphology	
Heart weight (% body weight)		
Sparrows	1·34, 0·19 (5)	—
Mice	0·50, 0·02 (5)	—
Lung weight (% body weight)		
Sparrows	0·74, 0·08 (5)	—
Mice	0·65, 0·08 (5)	—

#### *Oxygen dissociation curves*

The mean dissociation curve for sparrow blood at a temperature of 41·0° C. and a pH of 7·502 had a typical sigmoid appearance when plotted as percent saturation against P<sub>O<sub>2</sub></sub> (Fig. 1, Table 2).

The Bohr effect was characterized by a linear relation between log p<sub>50</sub> and pH over a pH range of 7·346–7·900. The equation fitted to the data by the method of least squares is

$$\log p_{50} = 4\cdot571 - 0\cdot386 \text{ pH}$$

(standard error of estimate = 0·085, N = 10).

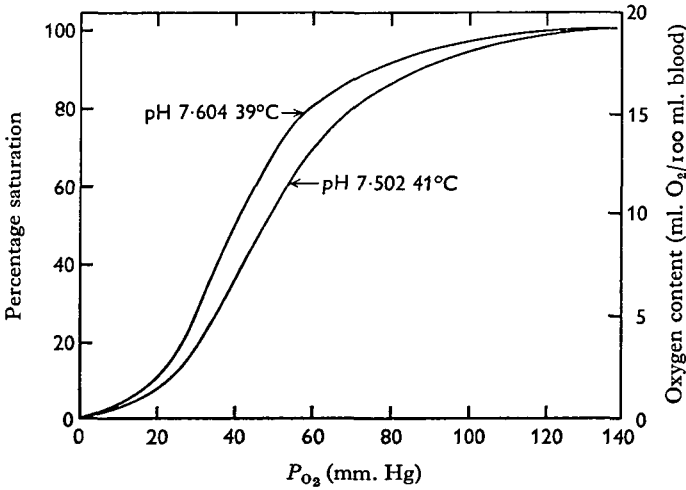


Fig. 1. Oxygen dissociation curves of house-sparrow blood. The right-hand curve describes the blood of birds at sea level (pH = 7.502, temp. = 41° C), the left-hand curve is for birds at 6100 m. (pH = 7.604, temp. = 39° C).

Table 2. Oxygen dissociation values for blood of house sparrows at pH 7.502 and 41.0° C. Log  $P_{O_2}$  values are means of eight observations. The standard error of the mean is given in parentheses. See text for explanation of units

	log $[Y/(100 - Y)]$			
	-1.00	-0.50	0.00	0.50
log $p_{O_2}$	1.346 (0.032)	1.524 (0.016)	1.676 (0.011)	1.817 (0.012)

#### Other results

The results of other measurements and calculations based on them are shown in Table 1.

#### Flight in the hypobaric chamber

Budgerigars in the wind tunnel could fly for 20 min. or more at sea level. At 3660 m. (12,000 ft.), they could fly at least 3 min. but would not make more than two such flights at 1 min. intervals. Above 3700 m. they would not fly as long as 3 min., and at 5500 m. (18,000 ft.) they would fly only a few seconds. The birds terminated their flights by landing on the floor of the wind tunnel. During and after flights at 3700 m. or more, they breathed with open mouths, but this was not observed at sea level.

The budgerigar wearing the oxygen mask was not tested for endurance, but it flew normally for 30 sec. at 6100 m. At 6700 m. (22,000 ft.) and more markedly at 7620 m. (25,000 ft.), the wind pushed it against the grill at the rear of the tunnel's working section.

Sparrows released at 6100 m. in the hypobaric chamber were able to fly and gain altitude at about 1 cm. per 10 cm. travelled forward. They did not fly spontaneously but were induced to fly by tossing them gently into the air. At 7620 m. the sparrows could fly but lost altitude at about 1 cm. per 10 cm. travelled forward. At 9140 m. (30,000 ft.), the sparrows could right themselves if turned over but could not stand, hop or fly.

## DISCUSSION

Compared to white mice, house sparrows are remarkably tolerant of an altitude of 6100 m. and an air temperature of 5° C. Sparrows exposed to these conditions could maintain both oxygen consumption and body temperature within the normal range for hours. Mice could not maintain their normal oxygen consumption under these conditions, and their body temperatures had dropped 10° C. after an hour of exposure.

The measurements on sparrows show how these birds adjust to low partial pressures of oxygen and suggest how birds flying at high altitudes obtain sufficient oxygen. The problem of oxygen supply can be broken into 3 parts: (1) getting oxygen through the lungs and into the blood, (2) transporting oxygenated blood to the tissues, and (3) getting oxygen from the blood to the tissues. Only parts 1 and 2 will be discussed in this paper.

*Oxygen movement through the lungs*

Sparrows at 6100 m. ventilate their lungs more rapidly than at sea level. A useful measure of ventilation is the 'effective ventilation', which is the same as alveolar ventilation in mammals. The latter term is inappropriate for birds since the avian lung has air capillaries rather than alveoli. During the respiratory cycle of a bird, some of the exhaled air has been in the air capillaries of the lungs and has undergone gas exchange with the blood. Another part of the exhaled air has simply moved through non-respiratory spaces. The air that has undergone gas exchange during one respiration is the effective tidal volume, and the effective tidal volume times the frequency of breathing is the effective ventilation, or that portion of the total ventilation that actually participates in gas exchange in the lungs.

When there is negligible CO<sub>2</sub> in inspired air, effective ventilation is calculated from the formula

$$\dot{V}_A = \frac{\dot{V}_{CO_2} (\text{barometric pressure})}{P_{ACO_2}}$$

(see Otis, 1964, for discussion) where  $\dot{V}_{CO_2}$  is the CO<sub>2</sub> production and  $P_{ACO_2}$  is the mean  $P_{CO_2}$  of the gas participating in effective ventilation. The variables of this equation can be estimated for sparrows from the measurements made in this study.  $\dot{V}_{CO_2}$  is calculated from oxygen consumption (assuming an R.Q. of 0.8).  $P_{ACO_2}$  usually is considered equal to the  $P_{CO_2}$  of arterial blood (Rahn & Farhi, 1964). The  $P_{CO_2}$  values for sparrows are from mixed arterial and venous blood and are higher than those for arterial blood. However, the arterial-venous  $P_{CO_2}$  difference in men using oxygen at 2.2 times the resting rate is small, being only about 7 mm. (Armstrong, Hurt, Blide & Workman, 1961). Accordingly,  $P_{ACO_2}$  of sparrows can be estimated as 3 mm. less than the  $P_{CO_2}$  of mixed arterial and venous blood, yielding a  $P_{CO_2}$  of 39.5 mm. at sea level and 27.2 mm. at 6100 m.

The estimates of effective ventilation at sea level and 6100 m. respectively are 80.3 and 142 ml. (g. hr.)<sup>-1</sup>, an increase of 78 % at high altitude. These figures are calculated for the volumes of gases that undergo gas exchange at the temperature, pressure and humidity prevailing in the bird's lungs. The corresponding dry-gas volumes at STP are 64.3 and 47.3 ml. (g. hr.)<sup>-1</sup> at sea level and 6100 m. respectively. Thus, at 6,100 m. even with hyperventilation, only 74 % as much oxygen enters the regions of the lungs where gas exchange occurs as at sea level.

The increase in effective ventilation at high altitude is about equally shared between increases in respiratory rate and in effective tidal volume. Mean respiratory rate increased by a factor of 1.4 at high altitude, requiring a multiplication of effective tidal volume by 1.3 to explain the changes in effective ventilation.

Since oxygen consumption is known it is possible to estimate the percentage of effective ventilation that represents oxygen utilization. At sea level the oxygen utilized comprises 7% of the effective ventilation. At 6100 m. the comparable figure is 12%. The corresponding values for a resting man at sea level and 6100 m. are similar, 8 and 12%, respectively (calculated from Otis, 1964, using figures for alveolar gas composition at sea level and altitude from Guyton, 1966, and assuming an R.Q. of 0.8).

#### *Oxygen transport*

All of the oxygen consumed by a sparrow must be transported by the cardiovascular system except for the small amount consumed by the respiratory parts of the lungs themselves. Oxygen transport is described by the equation

$$\text{oxygen consumption} = \text{heart rate} \times \text{stroke volume} \times AV \text{ difference,}$$

where the last factor is the difference in oxygen contents of arterial and mixed venous blood. Since simultaneous measurements of oxygen consumption and heart rate are available for sparrows, stroke volume (the blood pumped per heart beat) could be determined if the *AV* difference were known. Cardiac output (the product of heart rate and stroke volume) then could be determined.

Although the data do not permit exact determinations of cardiac output and stroke volume for sparrows, minimum values for these parameters can be calculated by considering the maximum values that *AV* difference can attain. The maximum value of *AV* difference must be less than the oxygen content of blood in equilibrium with the partial pressure of oxygen in the effective ventilation ( $P_{A_{O_2}}$ ) because the oxygen content of venous blood cannot fall to 0, and arterial blood coming from the lungs does not attain complete equilibrium with  $P_{A_{O_2}}$  in man and probably does not in sparrows.  $P_{A_{O_2}}$  is calculated from oxygen consumption and effective ventilation (R.Q. = 0.8) (Otis, 1964).

The oxygen content of blood in equilibrium with  $P_{A_{O_2}}$  can be determined from oxygen dissociation curves and the oxygen capacity of blood. At sea level the sparrows had a  $P_{A_{O_2}}$  of 99.7 mm. compared to 28.3 mm. at 6100 m. Referring to the oxygen dissociation curve (Fig. 1) for sparrows at sea level (pH = 7.502, body temperature 41° C.) it can be seen that arterial blood would be 94% saturated if it came into equilibrium with  $P_{A_{O_2}}$ . At 6100 m. (pH = 7.604, body temperature = 39° C.), arterial blood would be only 24% saturated with oxygen if it came into equilibrium with  $P_{A_{O_2}}$ . These percentages correspond to oxygen contents of 18.0 and 4.6 ml./100 ml. blood at each altitude, respectively.

The values for percentage saturation and maximum oxygen content of blood at 6100 m. indicate two peculiarities of sparrows that allow them to tolerate temperature and altitude conditions that some mammals cannot. First, the sparrows appear normal with a saturation of arterial blood with oxygen well below 40%, whereas this level marks the limit below which a man who is not acclimated to high altitudes becomes unconscious (Guyton, 1966). Second, sparrows appear capable of larger values of



stroke volume and cardiac output per kg. body weight than mammals. At 6100 m. the sparrows must have an  $AV$  difference less than 4.6 ml.  $O_2/100$  ml. blood, a stroke volume greater than 2.6 ml./kg. and a cardiac output greater than 1.88 l. (kg. min.)<sup>-1</sup>. Small mammals at rest have stroke volumes between 0.5 and 1.0 ml./kg. (Spector, 1956; Popovic & Kent, 1964) and judging from data on men and dogs (Astrand, Cuddy, Saltin & Sternberg, 1964; Cerretelli *et al.* 1964), these values may double during exercise. Cardiac outputs for men and dogs undertaking exercise are 0.31 and 0.52 l. (kg. min.)<sup>-1</sup>, respectively. Thus, the sparrows have stroke volumes that may be double the mammalian maximum, and cardiac outputs that are at least triple those of man and dogs. This enables them to transport oxygen at a relatively high rate even though their arterial blood has a low oxygen saturation.

Other data also indicate that birds have higher cardiac outputs than mammals. The relative weight of a sparrow heart is 2.7 times that of a mouse (Table 1). A high heart weight suggests a large energy expenditure for pumping blood which in turn suggests a high cardiac output. Calculations based on the oxygen consumption of flying budgerigars show that these birds can have cardiac outputs greater than 3.75 l. (kg. min.)<sup>-1</sup> (Tucker, 1966), almost double the estimate for sparrows at 6100 m. and more than 7 times the maximum for man and dogs.

#### *Flight at high altitudes*

Although the measurements in this study were made on birds that were not flying, and probably never fly at an altitude of 6100 m., they provide insight on how other birds might fly at this altitude. House sparrows at 6100 m. obtain oxygen at 2.2 times the resting level by hyperventilating and allowing their body temperatures to drop almost 2° C. These changes bring more oxygen to the lungs and increase the affinity of the blood for oxygen. A conservative estimate for oxygen consumption in flight is 8 times the resting level, and it is interesting to consider whether hyperventilation could be augmented to provide the additional oxygen required in flight. The estimates that follow suggest that a hypothetical sparrow could obtain adequate oxygen for flight at 6100 m. with values for ventilation and cardiac output that are reasonable in comparison with what is known of other birds.

Values for effective ventilation and cardiac output can be calculated for a hypothetical sparrow flying at 6100 m. if estimates are made for oxygen consumption, R.Q. and  $P_{ACO_2}$ . Oxygen consumption at 8 times the nocturnal, basal level in house sparrows is 20 ml.  $O_2$  (g. hr.)<sup>-1</sup> (King & Farner, 1960). R.Q. is assumed to be 0.8. A reasonable estimate of  $P_{ACO_2}$  is 20 mm., and lower values may be possible since arterial blood in pigeons can have a  $P_{CO_2}$  as low as 8.1 mm. during hyperventilation (Calder & Schmidt-Nielsen, 1966). These figures yield a value for effective ventilation of 695 ml. (g. hr.)<sup>-1</sup>. For a 23 g. bird, this ventilation could be achieved with an effective tidal volume of 0.75 ml. and a respiratory rate of 355/min.

These respiratory values for the hypothetical sparrow are reasonable in comparison with other birds in flight at sea level. A flying budgerigar weighing 40 g. has a total tidal volume greater than 1.3 ml/breath and a respiratory rate as high as 300/min. (Tucker, 1968). A flying pigeon weighing 360 g. has a total tidal volume of 5 ml./breath and a respiratory rate of 487/min. (Hart & Roy, 1966).

The cardiac output of the hypothetical sparrow is also reasonable in comparison

with the budgerigar.  $P_{\text{AO}_2}$  of the sparrow would be 41.7 mm. Arterial blood in equilibrium with this value at a  $P_{\text{CO}_2}$  of 20 mm. and a temperature of 39.4° C. would be 63 % saturated and would contain 12 ml.  $\text{O}_2$ /100 ml. blood. Since  $AV$  difference can not be greater than the oxygen content of arterial blood, the cardiac output of the hypothetical sparrow would have to be greater than 2.78 l. (kg. min.)<sup>-1</sup>. Flying budgerigars may have cardiac outputs above 3.75 l. (kg. min.)<sup>-1</sup> (Tucker, 1966).

Another problem of flight at 6100 m. is an aerodynamic one. Density of air at this altitude is only 53 % that at sea level, and the density of air affects the forces generated by motion of the air relative to a solid body. The observations in the hypobaric chamber on sparrows and budgerigars show that these birds are aerodynamically but not physiologically capable of flight at 6100 m. It is interesting that the budgerigar at this altitude required supplemented oxygen before it could meet the energy demands of flights lasting longer than a few seconds. Without supplemented oxygen it is doubtful whether a budgerigar could fly much higher than 3100 m.

It is clear that some birds fly at remarkably high altitudes. Why should this habit have evolved? With the exception of birds living in mountains it is difficult to see how high-altitude flight could directly influence reproductive physiology, predator avoidance, or food gathering, but conceivably it could affect the navigation abilities and energy requirements of migrating birds. Some birds obtain directional information from the sun and stars (Schmidt-Koenig, 1965), and high-altitude flight could keep these birds above cloud cover. High-altitude flight could reduce the energetic cost of migration by enabling birds to fly over rather than around mountains and to take advantage of horizontal air currents. Winds at high altitudes generally have higher speeds than those near the ground, and in some regions, low-level jet streams with speeds over 100 km./hr. could be reached by birds flying at 5500 m. or more (Reiter, 1963). A bird flying with such a jet stream could triple its ground speed, but on the other hand, flight against the wind would move the bird backwards twice as fast as it was flying. Thus, a bird would seem to need a sense of ground velocity before it could use or even avoid winds or jet streams to decrease the cost of migration. The operating principles of a biological ground-velocity sensor that could work at night from altitudes above 5500 m. are difficult to imagine.

Vertical air currents also could influence the energy requirements of migration. Standing waves in the atmosphere form parallel to and in the lee of mountain ranges and reach to altitudes well above 6100 m. (Wallington, 1961). Birds, like sailplane pilots, could use the strong updrafts on the wave front to coast along the mountain range.

The low temperature and density of air at high altitudes may influence the migration of birds, but no information is available on how these properties affect the energetic cost of avian flight.

#### SUMMARY

1. Some birds perform the strenuous activity of flapping flight at altitudes in excess of 6100 m. (20,000 ft.), an altitude at which resting, unacclimated man is in a state of incipient hypoxic collapse. This study investigates the respiratory problems associated with avian flight at 6100 m.

2. House sparrows and white mice were exposed to a simulated altitude of 6100 m.

for an hour. Their metabolic rates were kept above the basal level by regulating environmental temperature at 5° C. At 6100 m. the sparrows consumed oxygen at 2.2 times the basal rate, used more oxygen and had higher heart and respiratory rates than at sea level. Body temperature decreased 2° C., but the birds were normally active. In contrast, the mice at 6100 m. were moribund and had body temperatures 10° C. below normal after 1 hr. Oxygen consumption and respiratory rates were less than at sea level.

3. At 6100 m. sparrows ventilated the respiratory parts of their lungs 77% more than at sea level. At sea level and 6100 m. respectively, the partial pressure of carbon dioxide in the lungs dropped from 39.5 to 27.2 mm. Hg, and the partial pressure of oxygen in the lungs dropped from 100 to 28 mm. The sparrows removed a greater proportion of the oxygen from the air ventilating the lungs at 6100 m. than they did at sea level.

4. Oxygen dissociation curves were determined for sparrow blood at various pH values. At 6100 m. the arterial blood of sparrows appears to be less than 24% saturated with oxygen. For the cardiovascular system to transport adequate oxygen to the tissues at this low level of saturation house sparrows must have a cardiac output that is at least triple the maximum known for mammals.

5. House sparrows in a hypobaric chamber could fly 2.5 m. and gain altitude at a simulated altitude of 6100 m. but not at 7620 m. (25,000 ft.). Budgerigars trained to fly in a wind tunnel in the hypobaric chamber could fly more than 20 min. at sea level and a maximum of 3 min. at an altitude of 3660 m. (12,000 ft.). A budgerigar trained to wear an oxygen mask while flying in the wind tunnel could fly at an altitude of 6100 m.

6. Calculations based on our present knowledge of avian physiology suggest how birds could be capable of flying at 6100 m. The possible advantages of flight at high altitudes are discussed.

## REFERENCES

- ARMSTRONG H. G. (1952). *Principles and Practices of Aviation Medicine*. Baltimore: Williams and Wilkins Co.
- ARMSTRONG P. W., HURT, H. H., BLIDE, R. W. & WORKMAN, J. M. (1961). The humoral regulation of breathing. *Science* **133**, 1897-906.
- ASTRAND, P., CUDDY, T. E., SALTIN, B. & STERNBERG, J. (1964). Cardiac output during submaximal and maximal work. *J. appl. Physiol.* **19**, 268-74.
- ASTRUP, P. (1956). A simple electrometric technique for the determination of carbon dioxide tension in blood and plasma, total content of carbon dioxide in plasma, and bicarbonate content in 'separated' plasma at a fixed carbon dioxide tension (40 mm. Hg). *Scand. J. clin. Lab. Invest.* **8**, 33-43.
- ASTRUP, P. (1958). Ultra-micro-methods for determining pH, pCO<sub>2</sub> and standard bicarbonate in capillary blood. *Radiometer*, Copenhagen.
- AYMAR, G. C. (1935). *Bird Flight*. New York: Dodd, Mead Co.
- BROWN, W. E. L. & HILL, A. V. (1923). The oxygen-dissociation curve of blood, and its thermodynamical basis. *Proc. Roy. Soc. B* **94**, 297-334.
- CALDER, W. A. & SCHMIDT-NIELSEN, K. (1966). Evaporative cooling and respiratory alkalosis in the pigeon. *Proc. nat. Acad. Sci. U.S.A.* **55**, 750-56.
- CERRETELLI, P., PIIPER, J., MANGILI, F., CUTTICA, F. & RICCI, B. (1964). Circulation in exercising dogs. *J. appl. Physiol.* **19**, 29-32.
- DEPOCAS, F. & HART, J. S. (1957). Use of Pauling oxygen analyser for measurement of oxygen consumption of animals in open-circuit systems and in short-lag closed-circuit apparatus. *J. appl. Physiol.* **10**, 388-92.
- GUYTON, A. C. (1966). *Textbook of Medical Physiology*. Philadelphia: W. B. Saunders Co.
- HART, J. S. & ROY, O. Z. (1966). Respiratory and cardiac responses to flight in pigeons. *Physiol. Zool.* **39**, 291-306.

- HUNT, J. (1954). *The Conquest of Everest*. New York: E. D. Dutton, Inc.
- KING, J. R. & FARNER, D. S. (1960). Energy metabolism, thermoregulation and body temperature. In Marshall, A. J., *Biology and Comparative Physiology of Birds*, vol. II, 215. New York: Academic Press.
- LACK, D. (1960). The height of bird migration. *Br. Birds* 53, 5-10.
- LASIEWSKI, R. C. (1963). Oxygen consumption of torpid, resting, active, and flying hummingbirds. *Physiol. Zool.* 36, 122-40.
- LE FEBVRE, E. A. (1964). The use of  $D_2O^{18}$  for measuring energy metabolism in *Columbia livia* at rest and in flight. *Auk*, 81, 403-16.
- LUFT, U. C. (1965). Aviation physiology—the effects of altitude. In Fenn, W. O. & Rahn, H. (ed.). *Handbook of Physiology*. Respiration vol. II, 1099-1145. Washington: Amer. Physiol. Soc.
- MANVILLE, R. H. (1963). Altitude record for mallard. *Wilson Bull.* 75 (1), 92.
- MEINERTZHAGEN, R. (1955). The speed and altitude of bird flight. *Ibis* 97, 81-117.
- NISBET, I. C. T. (1963). Measurements with radar of the height of nocturnal migration over Cape Cod, Massachusetts. *Bird Banding* 34, 57-67.
- OTIS, A. B. (1964). Quantitative relationships in steady-state gas exchange. In Fenn, W. O. & Rahn, H. (ed.) *Handbook of Physiology*, Respiration, vol. I, 681-98. Washington: Amer. Physiol. Soc.
- POPOVIC, V. & KENT, K. M. (1964). 120-day study of cardiac output in unanesthetized rats. *Am. J. Physiol.* 207, 767-70.
- PROSSER, C. L. (ed.) (1950). *Comparative Animal Physiology*. Philadelphia: W. B. Saunders Co.
- PUGH, L. G. C. E. (1958). Muscular exercise on Mount Everest. *J. Physiol.* 141, 233-61.
- RAHN, H. & FARHI, L. F. (1964). Ventilation, perfusion, and gas exchange—The  $V_A/Q$  concept. In Fenn, W. O. & Rahn, H. (ed.), *Handbook of Physiology*. Respiration, vol. I, 735-66. Washington: Amer. Physiol. Soc.
- REITER, E. R. (1963). *Jet-Stream Meteorology*. Chicago: Univ. Chicago Press.
- SEVERINGHAUS, J. W., STUPFEL, M. & BRADLEY, A. F. (1956a). Accuracy of blood pH and  $pCO_2$  determinations. *J. appl. Physiol.* 9, 189-96.
- SEVERINGHAUS, J. W., STUPFEL, M. & BRADLEY, A. F. (1956b). Variations of carbonic acid  $pK'$  with pH and temperature. *J. appl. Physiol.* 9, 197-200.
- SCHMIDT-KOENIG, K. (1965). Current problems in bird orientation. In Lehrman, D. S., Hinde, R. A. & Shaw, E. (ed.), *Advances in the Study of Behavior*, 217-78. New York: Academic Press.
- SPECTOR, W. S. (ed.) (1956). *Handbook of Biological Data*. Philadelphia: W. B. Saunders Co.
- TUCKER, V. A. (1966). Oxygen consumption of a flying bird. *Science* 154, 150-51.
- TUCKER, V. A. (1967). Method for oxygen content and dissociation curves on microliter blood samples. *J. appl. Physiol.* 23, 410-14.
- TUCKER, V. A. (1968). Respiratory exchange and evaporative water loss in the flying budgerigar. *J. Exp. Biol.* 48, 67-87.
- WALLINGTON, C. E. (1961). *Meteorology for Glider Pilots*. London: J. Murray.