ARTERIAL BLOOD GASES AND RESPIRATORY RESPONSE TO SIMULATED HIGH ALTITUDE HYPOXIA IN THE PIGEON (*COLUMBA LIVIA*)

by

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ABSTRACT

Adult wild pigeons were exposed to low oxygen mixtures simulating altitudes of 2500 m, 4000 m, 5100 m, 6200 m, and 7400 m, and to a local altitude of 700 m. Arterial blood gases, heart rate and respiratory frequency were measured from unrestrained, unanesthetized birds. At progressively higher simulated altitudes respiratory frequency increased in response to lowered inspired P_{O_2} resulting in decreased arterial P_{CO_2}, presumably from the hyperventilation. The relationship of $P_{A_{O_2}}$ versus $P_{A_{CO_2}}$ was similar to man. Thus the avian system showed no advantage for preventing hypocapnic disturbance of blood arterial P_{CO_2} over the mammalian system.

The problem of O_2 consumption by avian nucleated erythrocytes during the interval required for membrane equilibration of blood gas analysis is discussed.

INTRODUCTION

Ventilation of the respiratory system occurs mainly for the purpose of exchanging oxygen and carbon dioxide between the blood and the external environment. Normal ventilation during rest maintains homeostasis of the gases in the blood and, secondarily to regulating P_{CO_2}, also functions in the maintaining of acid-base balance (see List of Symbols for explanation of abbreviations). Hyperventilation occurs in response to several conditions. Increased ventilation during exercise supplies oxygen for increased O_2 consumption and removes the extra CO_2 produced. Hyperventilation during thermal stress and low oxygen exposure, however, may not lead to a maintenance of blood P_{O_2} and P_{CO_2}. Thermal panting for evaporative cooling can occur when there is no respiratory need for increased ventilation. While the effect of P_{aO_2} is only to more fully saturate the blood which is nearly saturated normally, the resulting washout of CO_2 can have a marked effect on acid-base balance. This is well documented in mammals (Richards 1970).

Compared to the mammalian respiratory system the avian system has marked structural differences that suggest a possibly physiologically advantageous mechanism for thermal panting. The avian lung is essentially rigid and considerably smaller in volume than the lung of a comparably sized

mammal. In non-passerine birds, however, the tidal volume and minute volume are slightly greater than for similar sized mammals (Lasiewski and Calder 1971). This is made possible by the voluminous air sacs which occupy a large portion of the body cavity and have connections to the primary bronchus or directly to the lung. These air sacs allow unidirectional air flow through the lung parenchyma during both inspiration and expiration (Bouverot and Dejours 1971, Scheid and Piiper 1971, Bretz and Schmidt-Nielsen 1971, Brackenbury 1971). Schmidt-Nielsen et al. (1969) postulated the air sacs could provide an avenue for nonrespiratory ventilation that would allow increased air flow to the air sacs for the purpose of evaporative cooling but not through the lung where alkalosis would result. This was found to be the case in the ostrich (Schmidt-Nielsen et al. 1969) but other birds measured could not preserve CO_2 during panting and marked alkalosis occurred (Calder and Schmidt-Nielsen 1968).

During hyperventilation to obtain O_2 in the rarefied air at high altitude CO_2 washout occurs in man to such an extent that the resulting alkalosis prevents further increased ventilation until renal compensation occurs (Rahn and Otis 1949). Complete blood gas studies on birds acutely exposed to high altitude are not available but the literature indicates that birds tend to function better at altitude than mammals. Mountain climbers on Mount Everest, after several weeks of acclimatization, were capable of only minimal

exertion at 7900 m, yet they observed birds flying at the same altitude (Hunt 1953). In a laboratory comparison of a sparrow and a mouse made at a simulated altitude of 6100 m both survived the exposure. However, the sparrows remained active and alert and maintained body temperature only 2 °C below normal, while the mice became comatose, dropped body temperature 10 °C and reduced oxygen by half (Tucker 1968). The marked lowering of body temperature in response to low ambient P_{O_2} has also been measured in white rats where it is directly related to survival (Bartlett and Altland 1959).

It is tempting to suppose that the avian respiratory system provides some advantage for functioning at low oxygen partial pressures. Therefore, wild pigeons, unanesthetized and unrestrained, were subjected to simulated high altitudes and $P_{a_{CO_2}}$, $P_{a_{O_2}}$, pH, f and f_h were measured in an attempt to get a more complete picture of avian response to acute low oxygen exposure and to see if there is indeed an advantage in the avian respiratory system for providing oxygen or preserving carbon dioxide thus explaining birds superior functioning at high altitude.

MATERIALS AND METHODS

Pigeons

Wild pigeons were trapped at the University dairy farm and housed in a large outdoor aviary until the day prior to the experiment when they were brought into the laboratory. Weights ranged from 290 g to 510 g (mean 375 g). At least several hours prior to an experiment a catheter of polyethylene tubing with i. d. 0.58 mm (Intramedic PE-50) was inserted into a brachial artery for blood sampling. The surgical procedure was carried out under local anesthetic (2% lidocaine) while the bird was restrained on its side. A black cloth over the bird's eyes rendered it docile and there was no struggling. The catheter was flushed with heparinized (30 units/cc) avian physiological saline to prevent clotting.

Experimental Chamber

The chamber (Figure 1) was constructed of plexiglass covered with black paper to keep out light. A small hole was made in the top to accommodate electrode wires and the blood-sampling catheter. A wire mesh platform 3 cm above the floor of the chamber and a wire covered wooded dowel provided perching for the bird and were also wired to serve as ground for f and f_h recordings. Gas inlet was through the funnel at the front of the chamber. The birds tended to perch on the

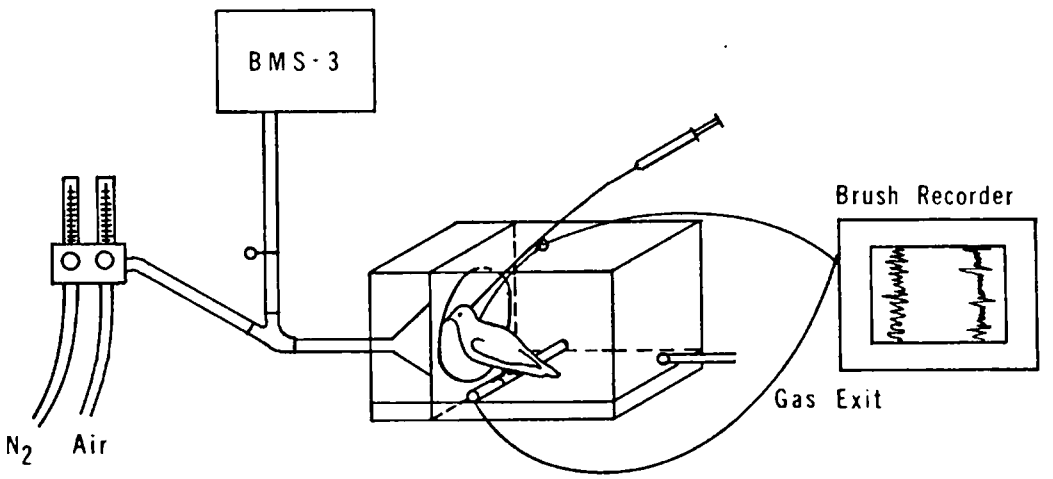

Figure 1. Apparatus

wooden dowel with their heads partially in the funnel, perhaps due to light viewed through the tip of the funnel at the gas inlet.

Gas Mixtures

Compressed air and nitrogen were mixed in a Simet Model 1517 gas mixer (National Welding Equipment Company) to produce the desired low O_2 concentrations. Flow meters of 0 - 57 l/min and 0 - 66 l/min were used for air and nitrogen, respectively. The graduations on the mixer flow meters were recalibrated to allow the use of inlet pressures lower than manufacturers specifications. Because the desired gas mixtures could not always be exactly reproduced, the P_{O_2} of the mixtures was measured with the oxygen electrode of the blood gas analyser described below during every experiment before the blood sample at each simulated altitude was drawn. For convenience, the gas for this procedure was taken from the line between the mixer and the chamber inlet rather than at the outlet. The volume of the chamber was 12.5 liters and gas flow was approximately 5 liters per minute. Therefore, if the flushing were perfect, the P_{O_2} of the chamber could reach a new steady-state within 3 minutes of starting a new gas mixture. Measurement of the outlet gas at 6 minutes showed that 95% of the change from the initial P_{O_2} to the new level had been obtained. At 15 minutes outlet P_{O_2} was within 1 mm of the inlet value. The P_{O_2} values for the gas

mixtures and the corresponding simulated altitudes are listed in the chart below.

P_{O_2}, mm Hg	49.5	60.5	72.0	85.5	105.5	135
Altitude, m	7400	6200	5100	4000	2500	700

Lowering of chamber P_{O_2} due to oxygen consumption of the bird was calculated using Butler's (1970) $\dot{V}_{O_2}$ value of 10 ml O_2 per minute. The maximum decrease calculated for P_{IO_2} was 1.2 mm Hg, assuming uniform mixing. Since the birds tended to have their heads at the inlet funnel they probably did not inhale the maximally decreased O_2 mixture.

Course of Experiment

Skin electrodes were attached to the axillary apterygium on one side of the bird and to the apterygium on the keel of the opposite side. The area was first cleansed with alcohol to remove oil and Skin Bond Cement (United Surgical Corporation) was used to hold the electrodes to the skin. The bird was then placed in the chamber. One half to one hour was allowed for the bird to settle down before the first blood sample was drawn. Preliminary experiments showed that the blood gas values had attained the new value within 15 minutes of starting a new gas mixture and values at 30 minutes were not significantly different at the 0.05 level than those at 15 minutes. Heart rate and respiratory rate were recorded at 15 minutes just prior to blood sampling. A blood

sample of about 0.2 ml in a 1 cc tuberculin syringe which had the dead space filled with heparinized (30 units/cc) avian saline. The syringe was capped, mixed and iced until blood gas determinations were made, within 90 minutes. Oxygen consumption of chilled chicken blood reported in the literature is negligible (Besch 1966; Besch, Burton and Smith 1971). Measurement of blood gas values on pigeon blood showed no significant difference between freshly drawn blood and iced aliquots measured two hours later. Ten birds were used in one or two experiments each for a total of fifteen experiments. An experiment consisted of a bird exposed to each level of $P_{I_{O_2}}$ consecutively from highest (room air) to lowest value of $P_{I_{O_2}}$. Sixteen to 20 minutes were spent at each level. The bird was undisturbed throughout the experiment since the distal end of the blood sampling catheter extended outside the experimental chamber.

Hematocrit

Microhematocrits were drawn in triplicate with the first blood sample and spun on an International Equipment Company hematocrit centrifuge for 5 minutes for maximum pack.

Heart Rate and Respiratory Rate

Leads from the skin electrodes and the ground lead were connected to Brush patient cable 780154 with input to Brush Impedance Coupler Model 11-4307-06 for respiratory rate

and Bio-Tach Coupler Model 11-4307-03 for heart rate. Results were recorded on Brush 440 recorder.

Blood Gases

P_{aCO_2}, P_{aO_2} and pH were measured on a Radiometer BMS-3b blood micro system with Radiometer pH meter type PHM71. The unit consists of a micro pH electrode, P_{CO_2} electrode and P_{O_2} electrode in a thermostated water bath. Measurements were made at 40 °C.

RESULTS

The mean hematocrit was 48.7 ± 1.1 ($\bar{X}$ ± 1 SE). Hydrogen ion concentrations ($[H^+]$) were calculated from pH values. Results for each of P_{aCO_2}, P_{aO_2}, pH, $[H^+]$, f, and f_h were grouped within ranges of measured inspired P_{O_2} and means and standard errors were determined. These values are summarized in Table I and graphed in Figures 2-6. Inspired P_{O_2} ranges are expressed as horizontal bars in the graphs. The values within the ranges are expressed as the mean ± 1SE. Exponential equations to fit the data were calculated and the curves were plotted with a Hewlett-Packard 9125A XY Plotter. The general equation for an exponential curve is

$$y = y_{asymp} - ae^{-kt} \quad \text{(Riggs 1963, p. 138).}$$

For the data presented here $t = P_{IO_2}$ and y is the measured variable. For the case of $y = P_{aO_2}$, the y asymptote is 0, leaving the simple form of the equation, $y = ae^{-kt}$. For the other variables an appropriate y asymptote was chosen to obtain the best correlation coefficient (r). For example, for P_{aCO_2} a y asymptote of 28 results in r = -.9977. The value for the asymptote is close to the room air value of the variable. It appears as the first term of the equation of the curve. The second term describes the exponential change of the difference of the data points and the asymptote.

TABLE I. Summary of Data[a] Grouped within Ranges of Inspired P_{O_2}

Simulated Altitude (m)	$P_{I_{O_2}}$, mm Hg mean (range)	$P_{a_{CO_2}}$ (mm Hg) N = 15	$P_{a_{O_2}}$ (mm Hg) N = 15	f_h (beats/min) N = 7	f (breaths/min) N = 9	pH N = 11	$[H^+] \times 10^8$ (moles/l) N = 11
700	135 (134-136)	26.7 (0.4)	79.3 (0.9)	119.7 (5.9)	18.6 (1.1)	7.513 (.008)	3.07 (.063)
2500	105.5 (100-111)	24.9 (0.5)	58.3 (0.9)	122.2 (4.1)	20.2 (1.4)	7.530 (.011)	2.95 (.078)
4000	85.5 (81-90)	22.3 (0.5)	46.0 (0.9)	128.0 (6.0)	21.7 (1.3)	7.545 (.012)	2.85 (.075)
5100	72 (68-76)	20.6 (0.6)	38.7 (0.7)	148.1 (9.2)	26.1 (2.2)	7.565 (.012)	2.72 (.078)
6200	60.5 (56-65)	17.2 (0.4)	33.8 (0.7)	156.7 (7.8)	34.4 (2.8)	7.589 (.011)	2.58 (.069)
7400	49.5 (45-54)	15.2 (0.4)	30.8 (0.5)	161.7 (6.1)	40.7 (4.5)	7.606 (.012)	2.48 (.069)

[a]Mean with standard error (SE) in parenthesis under mean except for $P_{I_{O_2}}$ as indicated.

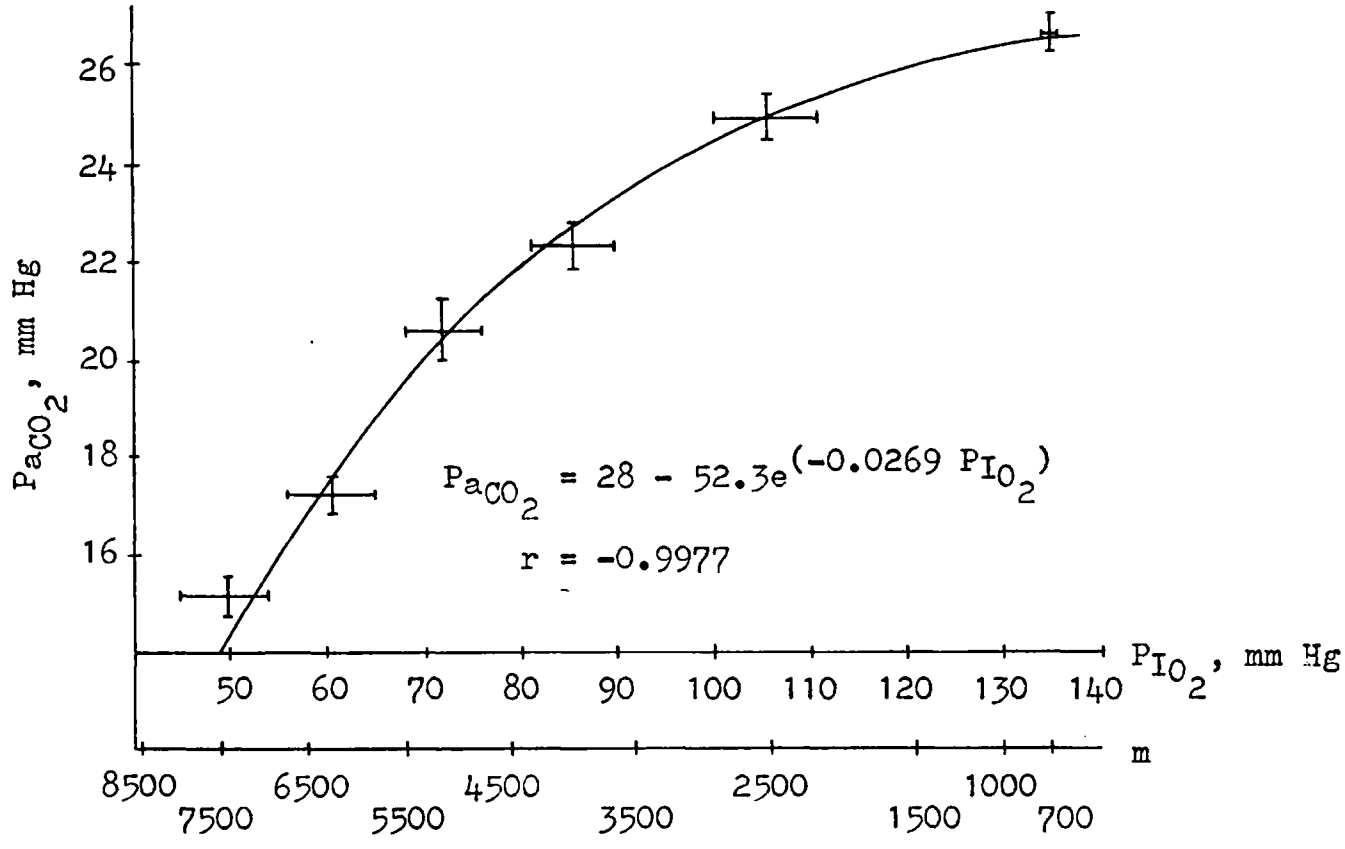

Figure 2. Arterial P_{CO_2} versus Inspired P_{O_2}.

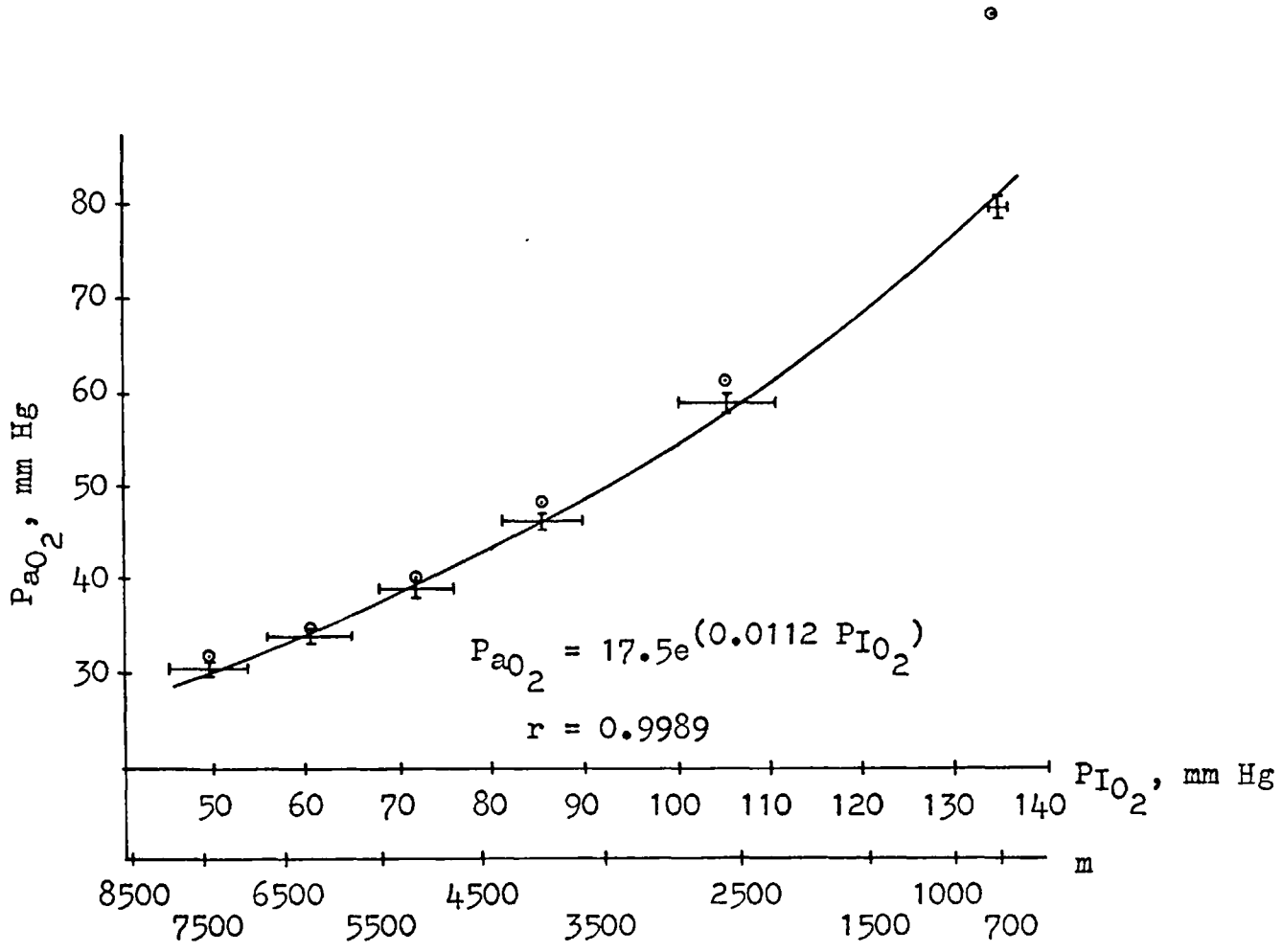

Figure 3. Arterial P_{O_2} versus Inspired P_{O_2}.

⊙'s indicate $P_{a_{O_2}}$ means corrected for oxygen consumption during blood gas analysis.

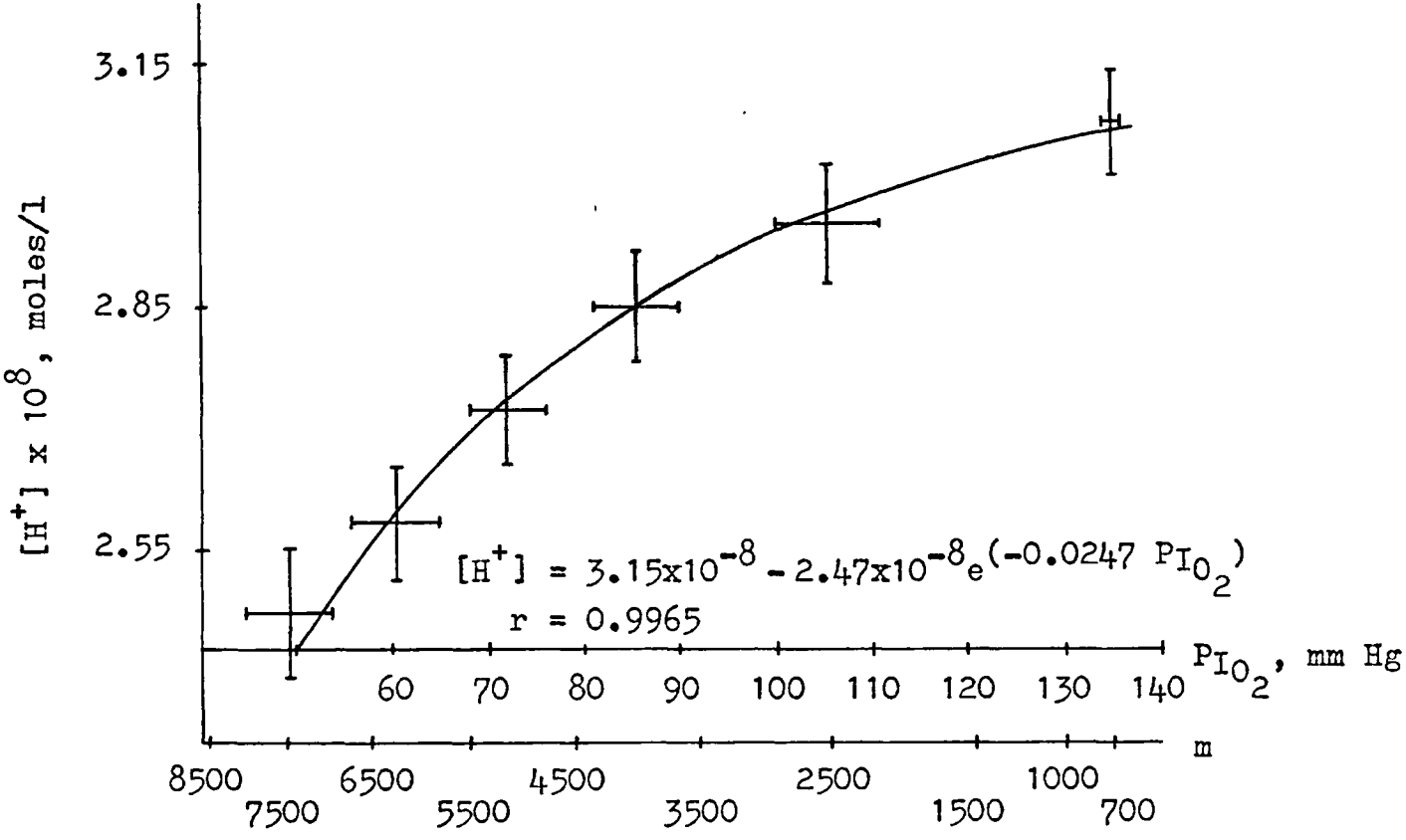

Figure 4. Arterial Hydrogen Ion Concentration versus Inspired P_{O_2}.

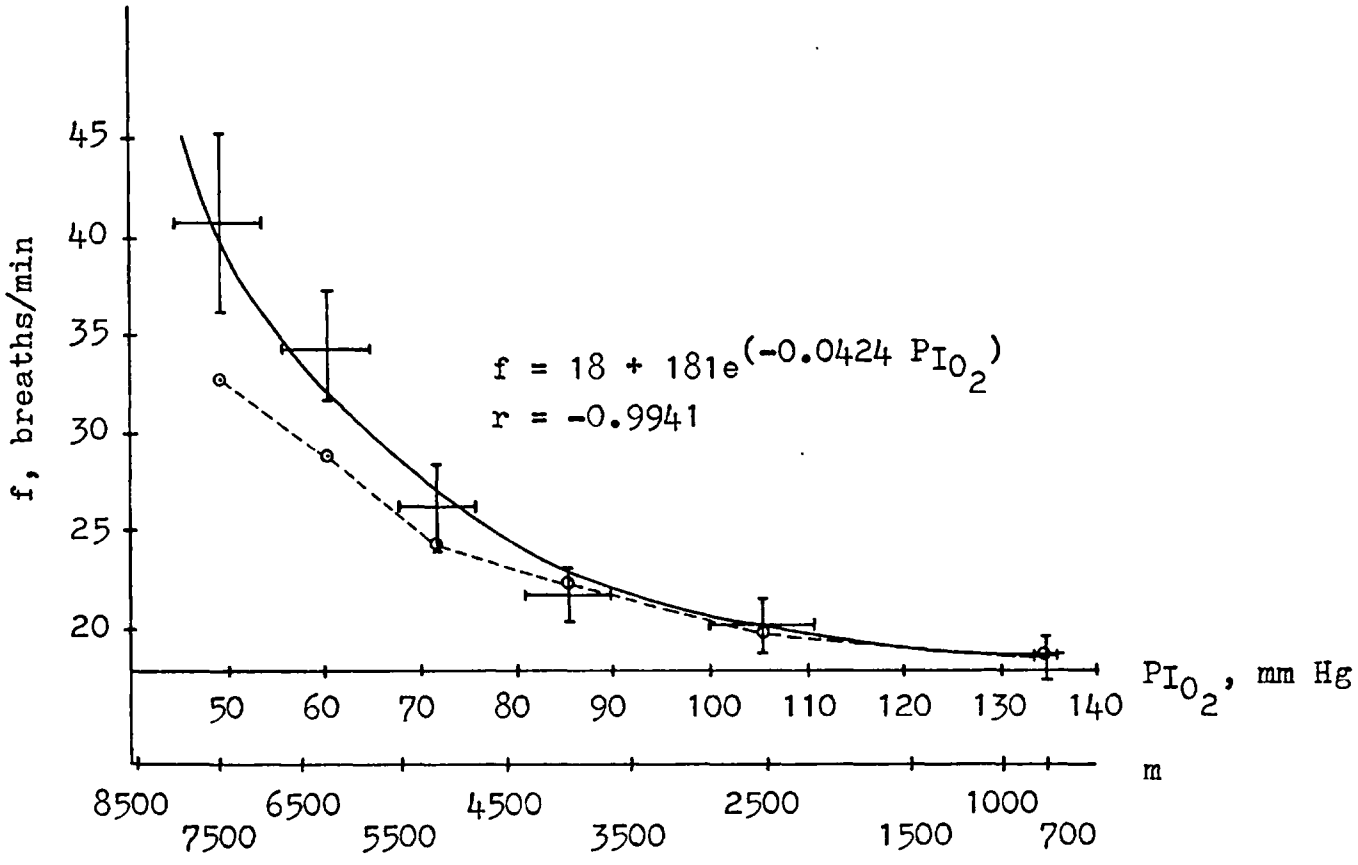

Figure 5. Respiratory Frequency versus Inspired P_{O_2}.

Dotted line and ⊙'s indicate calculated respiratory frequencies necessary to account for arterial P_{CO_2} (see text and Table II).

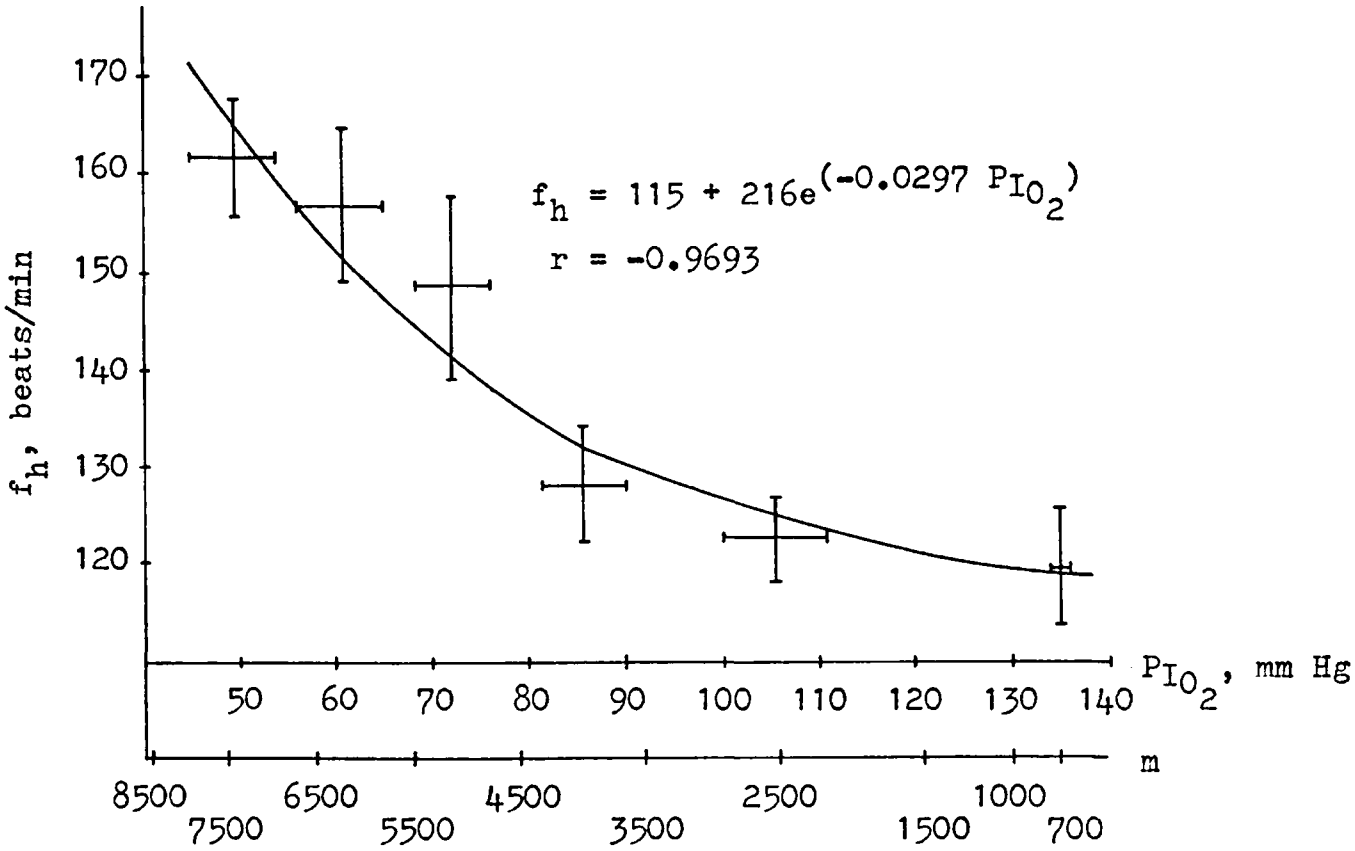

Figure 6. Heart Rate versus Inspired P_{O_2}.

At higher inspired oxygen pressures, P_{aCO_2} approaches the normal room air value for the bird. As the P_{IO_2} decreases, as it would in attaining high altitude, the difference between the measured P_{aCO_2} and 28 increases exponentially. Figure 2 shows that P_{aCO_2} decreases by larger increments as lower P_{O_2}'s are inspired. The same relationship is seen in Figure 4 for $[H^+]$. The decreases in P_{aCO_2} and $[H^+]$ indicate the occurrence of hyperventilation at simulated high altitude. Minute volume was not measured but the data for f (Figure 5) show an exponential increase in respiratory frequency at lower P_{IO_2} which may indicate hyperventilation.

The circulatory system also responded to the stress of low P_{IO_2} as noted by the exponential increase in heart rate (Figure 6) at simulated high altitudes.

DISCUSSION

Respiratory Response

The wide individual variation in respiratory response to lowered inspired P_{O_2} as noted in Figure 3 has also been measured in humans (Shock and Soley 1942, Dripps and Comroe 1947). The ventilatory response in humans was attributed largely to an increase in depth of breathing (Dripps and Comroe 1947). In hypoxia of anesthetized hens ventilated unidirectionally, both respiratory rate and amplitude increased, the greater effect being on rate (Ray and Fedde 1969). In the present study respiratory amplitude was not measured so no direct comparison of changes in rate and depth of breathing can be made. However, it is possible to calculate whether or not the measured f at each simulated altitude is sufficient to account for the increased ventilation necessary to produce the $P_{a_{CO_2}}$ measured at that altitude.

Fenn, Rahn and Otis (1946) give the following equation for effective (alveolar) ventilation:

$$\dot{V}_A = \frac{k \dot{V}_{O_2} R}{P_{A_{CO_2}}}$$

where k is a constant determined by body temperature. Assuming O_2 consumption to remain unchanged and R to have

returned to its "sea level" value at the time of measurement of P_{aCO_2} and using P_{aCO_2} in place of P_{ACO_2}, ventilation ratio can be calculated. If initial ventilation equals

$$\dot{V}_A^o = \frac{k\,\dot{V}_{O_2}^o\,R^o}{P_{ACO_2}^o}$$

and ventilation at a new steady state equals

$$\dot{V}_A = \frac{k\,\dot{V}_{O_2}\,R}{P_{ACO_2}}$$

then, letting $\dot{V}_A^o = 1$, the ventilation ratio for the new steady state is

$$\frac{\dot{V}_A}{1} = \frac{P_{ACO_2}^o}{P_{ACO_2}}$$

Table II shows the ventilation ratios calculated from the measured P_{aCO_2} values and the f (calculated from this ratio and the initial f) which one would expect to measure if the total increase in ventilation were due to increase in f. The calculated f are graphed along with the measured f in Figure 5. The calculated values in all cases fall within 1 SD of the mean measured values and indicate the measured f is indeed sufficiently large to account for the entire change in

TABLE II. Respiratory Ventilation Ratio and Calculation of Respiratory Frequency to Account for Measured Change in $P_{a_{O_2}}$

$P_{I_{O_2}}$	$P_{a_{CO_2}}$	Ventilation Ratio $\frac{P^{o}_{CO_2}}{P_{CO_2}}$	f	f calc (f^{o} x ventilation ratio)
135	26.67[a]	--	18.6[a]	--
105.5	24.87	1.07	20.2	19.9
85.5	22.27	1.20	21.7	22.3
72	20.61	1.30	26.1	24.2
60.5	17.18	1.55	34.4	28.8
49.5	15.24	1.76	40.7	32.7

[a]Initial value occurring at room air $P_{I_{O_2}}$.

measured $P_{a_{CO_2}}$. If the assumption of constant O_2 consumption is inaccurate and O_2 consumption is actually lower as suggested by Butler (1970) this relationship still holds true. However, if O_2 consumption were increased as would be the case if increased work were necessary for the greater ventilation, an increase in respiratory amplitude would also be indicated.

Oxygen Consumption During Blood Gas Analysis

The arterial P_{O_2} values measured while the pigeons were breathing room air are considerably lower than those reported by some other investigators for resting pigeons (Butler 1970, Sturkie 1965) or other birds (Piiper, Drees and Scheid 1970). This may in part be due to the 700 m altitude of Tucson which results in an inspired P_{O_2} (BTPS) of 135 mm Hg as compared to 147 mm Hg at sea level. Also, the handling of the blood samples may have resulted in lowered $P_{a_{O_2}}$ values. As noted previously, it has been determined that storing pigeon blood in ice water resulted in no significant change in the blood gas values. However, after introducing a sample to the measuring chamber of the blood gas analyser 45 seconds elapsed before the P_{O_2} reading was made. This interval is necessary to allow temperature equilibration and equilibration of P_{O_2} across the electrode membrane. Therefore,

the nucleated erythrocytes could consume oxygen as the blood warmed to 40 °C and reduce the P_{O_2}.

According to Lutz et al. (1973) O_2 consumption of bird blood is 1.04×10^{-3} ml $O_2 \cdot min^{-1} \cdot ml^{-1}$ or 1.04 vol % each minute at 40 °C. The O_2 capacity of blood can be calculated from its hemoglobin content. For the following calculations the hemoglobin concentration value of 19.4 g/100 ml blood measured by Bond and Gilbert (1958) for adult pigeons will be used. Each gram of hemoglobin, when saturated, holds 1.34 ml O_2 (Steen 1971, p. 7); therefore, the O_2 content is 26.0 ml O_2/100 ml blood or 26.0 vol %.

Column 2 in Table III lists % saturation values read off the O_2 dissociation curve of Lutz et al. (1973) that correspond to the measured P_{aO_2} values shown in column 1. The O_2 content (column 3) is calculated from the formula:

$$O_2 \text{ Content (Vol \%)} = \frac{\text{\% Sat} \times O_2 \text{ Capacity}}{100}$$

Birds breathing room air (P_{aO_2}, 79 mm Hg) had 98% O_2 saturation and an O_2 content of 25.5 vol %. One hundred percent saturated blood would have had an O_2 content of 26.0 vol %. Therefore, during a 45 second equilibration in the blood gas analyser, a maximum of 0.5 vol % O_2 could have been consumed. This is lower than the 45/60 x 1.04 = 0.77 vol % expected from Lutz et al. calculation of O_2 consumption for pigeon blood at 40 °C, but the blood in the analyser is cooler

TABLE III. Correction of Pa_{O_2} Values for O_2 Consumption of Red Cells During Blood Gas Analysis

1	2	3	4	5	6
Measured Pa_{O_2}	% Saturation[a]	O_2 Content[b] (vol %)	Corrected O_2 Content (vol %)	Corrected % Saturation[c]	Corrected[d] Pa_{O_2}
79.3	98	25.5	26.0	100	95-100
58.3	90	23.4	23.9	92	61
46.0	79	20.5	21.0	81	48
38.7	68	17.7	18.2	70	40
33.8	58	15.1	15.6	60	34.5
30.8	52	13.5	14.0	54	32

[a]Values read from graph of Lutz et al. (1973).

[b]Calculated from vol % = $\frac{\%\ \text{Sat.} \times O_2\ \text{Capacity.}}{100}$

[c]Calculated from corrected O_2 content.

[d]Read from graph of Lutz et al. (1973) and values in column 5.

than 40 °C for at least some of the interval and O_2 consumption is markedly reduced at lower temperatures (Besch 1966). A corrected P_{aO_2} is calculated (columns 4, 5 and 6) assuming the maximum 0.5 vol % O_2 consumption occurred in samples collected at each simulated altitude. These values are indicated on the graph of Figure 3. Only the values for room air conditions show a large difference between measured and corrected P_{aO_2} because in that instance the O_2 consumption is occurring at a P_{O_2} at which the O_2 dissociation curve has a very shallow slope and even a small change in O_2 content, and therefore O_2 saturation, will have a large effect on measured P_{aO_2}.

Richards and Sykes (1967) used a KCN-heparin mixture in blood sampling syringes to inhibit avian erythrocyte respiration. He measured a "resting" P_{aO_2} in anesthetized hens of 92 mm Hg. Other authors, however, did not employ respiratory inhibitors for avian blood gas studies (Scheid and Piiper 1972, Cohn and Shannon 1968). Interestingly, their results showed a $P_{EO_2} - P_{aO_2}$ difference of 19 mm Hg and 18 mm Hg, respectively, when P_{EO_2} was near 100 mm Hg. These differences are strikingly similar in magnitude to the P_{aO_2} change calculated here for O_2 consumption of pigeon blood during blood gas analysis.

The Oxygen-Carbon Dioxide Diagram

The relationship of human alveolar P_{O_2} to alveolar P_{CO_2} under varied conditions of altitude, R, and respiratory ventilation has been analysed extensively by Fenn, Rahn and Otis (1946). The oxygen-carbon dioxide diagram they used to describe this relationship is reproduced in part in Figure 7. The diagonal dashed lines are isoaltitude lines that predict the location of paired P_{AO_2} and P_{ACO_2} values at a specified altitude and R. For example, a man breathing air at 4000 m should have alveolar P_{O_2} and P_{CO_2} coordinates that will fall on the 4000 m isoaltitude line. An increase or decrease in alveolar ventilation will result in the paired coordinates being located lower and to the right or higher and to the left, respectively, along the same isoaltitude line. The predicted alveolar gas composition was supported by measured values by Rahn and Otis (1949). Their curves for unacclimatized and acclimatized man are included in Figure 7. The location of the curve for acclimatized man below that of unacclimatized man results from the increase in ventilation which is part of the acclimatization process.

Comparison of Pigeons and Man at High Altitude

Isoaltitude lines pertaining to my pigeon study were calculated from equation 7 of Fenn et al. (1946). Sample calculations are shown in Appendix I. Slightly different effects on alveolar air are obtained when high altitude is

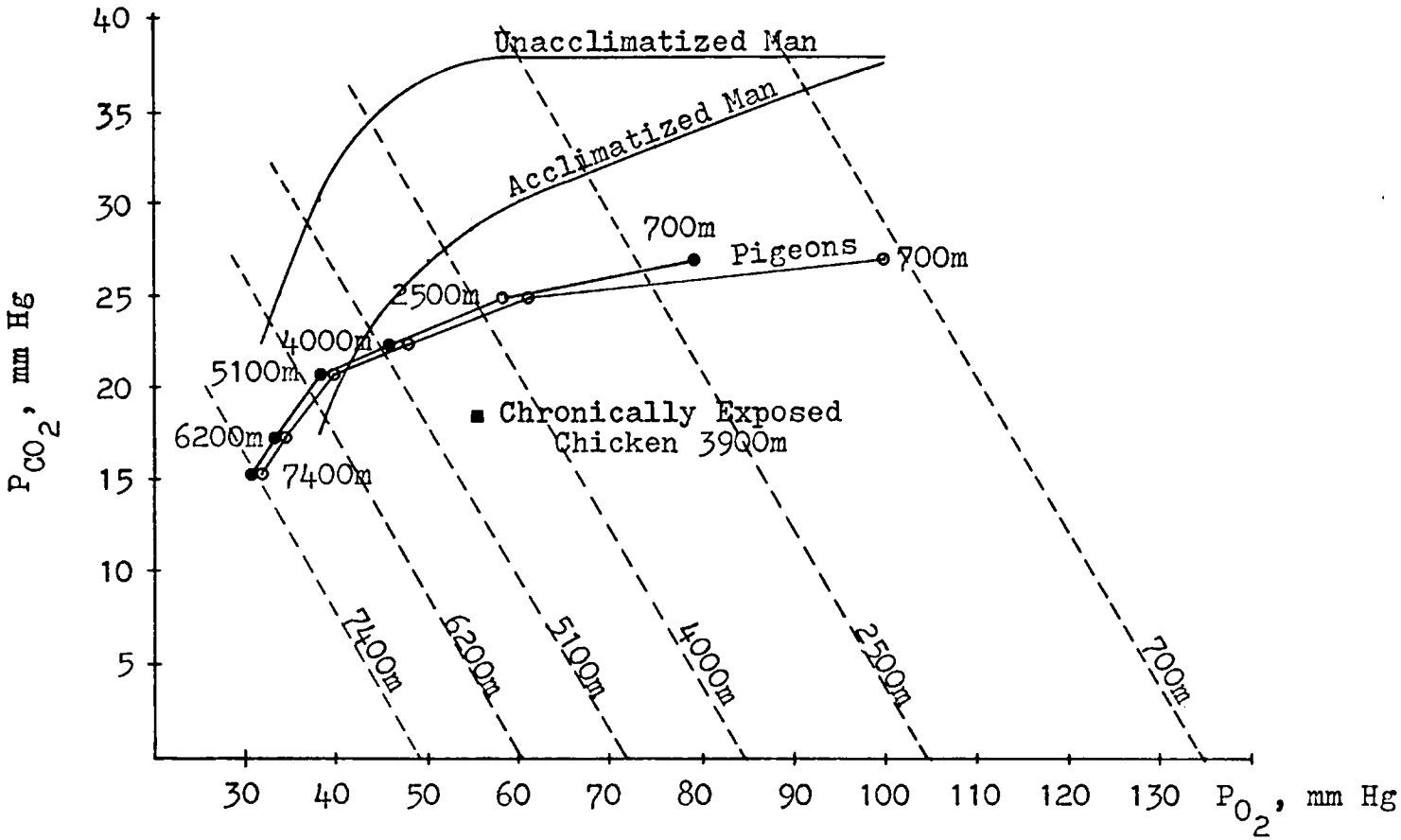

Figure 7. Pigeon Arterial Blood Gases Compared to Man's Alveolar Gases on the Oxygen-Carbon Dioxide Diagram.

● measured pigeon values, ○ pigeon values with corrected Pa_{O_2},
■ chronically exposed chicken at 3900 m (Besch et al. 1971).

simulated by low O_2 mixtures rather than under hypobaric conditions (Fenn et al. 1946). However, the isoaltitude lines for the conditions of this experiment are displaced only slightly to the right from the position they would have if 20.95% oxygen at low pressure were used instead. The difference is 0.5 mm Hg O_2 or less at the points where the isoaltitude lines cross the pigeon curve.

Since, in man, arterial blood is very nearly equilibrated with the alveolar gases, values can be taken from Figure 7, at the points where the isoaltitude lines cross the curves for acclimatized and unacclimatized man, to be used for comparison with pigeon arterial P_{O_2} and P_{CO_2}. These values are listed in Table IV. The pigeon P_{O_2} is approximately the same as P_{O_2} for unacclimatized man, while the corrected values tend to be slightly higher. In all instances the P_{O_2} for acclimatized man is higher than for unacclimatized man or pigeons. Thus it does not appear that unacclimatized pigeons have an advantage over man in supplying oxygen to the blood.

P_{CO_2} decreases markedly with altitude in both pigeons and man, but it is likely that the birds suffer somewhat less from loss of CO_2. In changing altitude from 700 m to 6200 m the P_{CO_2} of pigeons, unacclimatized man and acclimatized man changed 31%, 38%, and 53%, respectively. Although P_{CO_2} of

TABLE IV. Comparison of P_{O_2} and P_{CO_2} Values of Man and Pigeons at High Altitude

Altitude (m)	P_{O_2}, mm Hg			P_{CO_2}, mm Hg		
	Pigeons[a]	Man Unacclimatized	Man Acclimatized	Pigeons	Man Unacclimatized	Man Acclimatized
700	79.3(95-100)	--	--	26.7	38	--
2500	58.3(61)	60	67.5	24.9	38	31.5
4000	46.0(48)	44	52	22.3	34.3	27.5
5100	38.7(40)	37	44	20.6	28.7	23
6200	33.8(34.5)	33	39	17.2	23.5	18
7400	30.8(32)	--	--	15.2	--	--

[a]Measured P_{aO_2} (corrected P_{aO_2}).

pigeons is lower at 6200 m, it has changed by a proportionately smaller amount. Also, the lowest P_{CO_2} measured, 15.2 mm Hg, is considerably above the low value of 8 mm Hg measured during thermal panting (Calder and Schmidt-Nielsen 1966) which resulted in no apparent ill effect on the animal, at least for relatively short exposures (2.1 hrs.).

When the pigeon $P_{a_{O_2}}$ and $P_{a_{CO_2}}$ are plotted on the O_2-CO_2 diagram, for all altitudes except 7400 m, the measured $P_{a_{O_2}}$ is lower than that calculated by the alveolar ventilation equation for the corresponding measured $P_{a_{CO_2}}$. Therefore, the data points do not fall on the isoaltitude lines. Using the corrected $P_{a_{O_2}}$ values only partially compensates for this displacement except for the room air value. Data of other investigators for birds at sea level P_B are graphed in Figure 8. In general the end tidal values tend to fall near the sea level isoaltitude line. Where simultaneous data is available for both arterial blood and end tidal gases the arterial values are displaced further to the left of the isoaltitude line.

Unlike the situation in man, avian arterial blood gases can not be used to approximate "alveolar" gas values. $P_{a_{O_2}}$ is consistently lower than $P_{E_{O_2}}$ (Figure 8, also Cohn and Shannon 1968). $P_{a_{CO_2}}$ can be lower than $P_{E_{CO_2}}$—a condition that can be explained by the cross current arrangement of

avian parabronchi and lung blood capillary supply (Duncker 1972, Scheid and Piiper 1970).

Acclimatization in birds may be qualitatively similar to that in man, resulting in a lowered $P_{a_{CO_2}}$ and higher $P_{a_{O_2}}$. This is suggested by the difference between these pigeons acutely exposed to a simulated 4000 m and Besch, Burton and Smith (1971) chickens chronically exposed to 3900 m (see Figure 7).

Analysis of Tracheal Dead Space and Buffering of CO_2

The O_2-CO_2 diagram can be used to examine mathematically the concept of tracheal buffering of CO_2. The avian trachea has a larger dead space than that of mammals of comparable size and some birds have especially long tracheae (Hinds and Calder 1971, Portmann 1950). The oxygen requirement of flight is 11 to 20 times that at rest (Tucker 1969). This must be obtained, at least in part, by increased ventilation. Schmidt-Nielsen (1971 and personal communication) suggests that a possible function of the greater tracheal dead space is to allow retention of CO_2 during the high ventilation requirement of flight. This is not supposed to have the same result as simply breathing less deeply with a smaller dead space. According to Schmidt-Nielsen, by increasing the dead space and tidal volume so that their ratio remains the same, the case of the larger dead space supplies

a larger amount of gas at the same P_{O_2} and therefore more O_2 is available in the lung.

To analyse the theory numerically V_T, V_D, $\dot{V}_{O_2}$, and f values for an allometrically generalized 1 kg non-passerine were obtained from Lasiewski and Calder (1971). Values for gas composition of the trachea and end tidal values were from Piiper, Drees and Scheid (1970). One breath will be followed through the respiratory system. For simplicity I assume that the entire tidal volume flows into the posterior air sacs and then through the parabronchi before being expired.

Tidal volume for a 1 kg bird is 13.2 ml. Tracheal volume is 3.7 ml leaving 13.2 - 3.7 = 9.5 ml of fresh air in the inspired volume. The fresh air contains 9.5 x 0.2095 = 1.98 ml O_2 and essentially no CO_2. The end tidal (tracheal) gas would have a P_{O_2} of 102 mm Hg and P_{CO_2} of 33 mm Hg. The fractional values are 0.144 and 0.047, respectively. Therefore, the gas inspired from the dead space contains 3.7 x 0.144 = 0.53 ml O_2 and 3.7 x 0.047 = 0.17 ml CO_2. The mixture entering the posterior air sacs has 0.53 + 1.98 = 2.51 ml O_2 and 0.17 ml CO_2. The corresponding partial pressures, assuming P_B = 760 mm Hg and P_{H_2O} = 55 mm Hg are P_{O_2} = 133 mm Hg and P_{CO_2} = 9 mm Hg. When this mixture passes through the lung it will lose oxygen and gain carbon dioxide, the amount being dependent on metabolism per unit time and respiration per unit time. If $\dot{V}_{O_2}$ is 11.3 cc O_2/min and f is 17.2

breaths/min, then 11.3 ÷ 17.2 = 0.65 ml O_2 will be removed from each breath. Similarly, assuming an R of 0.8, 0.53 ml of CO_2 will be added per breath. The mixture leaving the lung, therefore, contains 1.86 ml O_2 and 0.70 ml CO_2 in a total volume of 13.1 ml gas. The corresponding pressures are 98.7 mm Hg P_{O_2} and 37.4 mm Hg P_{CO_2}. These figures are listed in Table V. When the calculations are repeated using a doubled tidal volume and doubled dead space volume, the partial pressures of the gases in the posterior air sacs remain the same but the mixture leaving the lung has a higher P_{O_2} and lower P_{CO_2}.

If the basis of respiration is to obtain oxygen and the initial conditions analysed are assumed to supply the necessary oxygen, the second case can be considered overventilation in terms of O_2. The $P_{E_{O_2}}$ value of 98.7 mm Hg, obtained with the initial V_T and V_D, can be produced with conditions of doubled V_T and V_D by changing the respiratory frequency to 8.7 breaths/min and adjusting $\dot{V}_{O_2}$/breath and $\dot{V}_{CO_2}$/breath accordingly. Following a breath through the bird respiratory system by repeating the above calculations reveals that reducing f as described to prevent the overventilation of oxygen produces the same P_{CO_2} (37.4 mm Hg) as the initial conditions. A P_{O_2} of 98.7 mm Hg leaving the lung can also be achieved by maintaining the doubled V_D and adjusting (lowering) the tidal volume. Again the resulting

TABLE V. Analysis of Single Breaths of Air Passing through the Avian Respiratory System

	"Normal"	2x "Normal"	adjusted f	adjusted V_T
Tidal volume (ml)	13.2[a]	26.4	26.4	16.3
Tracheal volume (ml)	3.7[a]	7.4	7.4	7.4
Fresh air (ml)	9.5	19.0	19.0	8.9
$F_{I_{O_2}}$	0.2095	0.2095	0.2095	0.2095
$P_{I_{O_2}}$ (mm Hg)	146	146	146	146
$F_{I_{CO_2}}$	0.0003	0.0003	0.0003	0.0003
$P_{I_{CO_2}}$ (mm Hg)	0	0	0	0
ml O_2 in fresh air	1.98	3.98	3.98	1.87
ml CO_2 in fresh air	0	0	0	0
$P_{D_{O_2}}$ (mm Hg)	102[b]	102	102	102
$F_{D_{O_2}}$	0.144	0.144	0.144	0.144
ml O_2 in dead space	0.53	1.06	1.06	1.06
$P_{D_{CO_2}}$ (mm Hg)	33[b]	33	33	33
$F_{D_{CO_2}}$	0.047	0.047	0.047	0.047
ml CO_2 in dead space	0.17	0.34	0.34	0.34
ml O_2 in posterior air sacs	2.49	4.98	4.98	2.93
P_{O_2}, posterior air sacs (mm Hg)	133	133	133	127

TABLE V. Continued

	"Normal"	2x "Normal"	adjusted f	adjusted V_T
ml CO_2 in posterior air sacs	0.17	0.34	0.34	0.34
P_{CO_2}, posterior air sacs (mm Hg)	9	9	9	14.7
$\dot{V}_{O_2}$ (ml O_2/min)	11.3[a]	11.3	11.3	11.3
$\dot{V}_{CO_2}$ (ml CO_2/min)	9.04	9.04	9.04	9.04
f (breaths/min)	17.2[a]	17.2	8.7	17.2
$\dot{V}_{O_2}$/breath	0.65	0.65	1.30	0.65
$\dot{V}_{CO_2}$/breath	0.53	0.53	1.06	0.53
ml O_2 leaving lung	1.86	4.33	3.68	2.28
ml CO_2 leaving lung	0.70	0.87	1.40	0.87
P_{EO_2} (mm Hg)	98.7	116	98.7	98.7
P_{ECO_2} (mm Hg)	37.4	23.3	37.4	37.4
F_{EO_2}	0.14	0.165	0.14	0.14
F_{ECO_2}	0.053	0.033	0.053	0.053

[a]Lasiewski and Calder (1971).

[b]Piiper, Drees and Scheid (1970).

$P_{E_{CO_2}}$ is 37.4 mm Hg. Therefore, the increase in tracheal volume cannot be shown to preserve P_{CO_2} at a more favorable $P_{a_{O_2}}$.

Several additional calculations of $P_{E_{O_2}}$ and $P_{E_{CO_2}}$ were made using different combinations of V_T and V_D (Table VI). The results, along with the values from the above discussion, were plotted on the O_2-CO_2 diagram (Figure 8). All data points lie on the predictive isoaltitude line.

Consequences of the Oxygen-Carbon Dioxide Diagram

The finding that birds, like mammals, must compromise the preserving of $P_{a_{CO_2}}$ in deference to obtaining oxygen in a low P_{O_2} environment is not a surprising one in view of the fact that gas exchange is dependent on the inspired medium (Rahn 1966), air, and the solubilities and diffusion properties of the gases involved. These are constant in both and increased ventilation for obtaining oxygen must result in increased loss of carbon dioxide. Similarly, the concept of tracheal buffering of CO_2 by increased dead space as suggested by Schmidt-Nielsen (1971) allows preserving CO_2 only at the expense of decreasing O_2 available for exchange.

A unique system has been postulated for the ruminants, which tend to partially restore $P_{a_{CO_2}}$ after its initial lowering at altitude. Lahiri et al. (1971) suggest the rumen, which maintains a very high P_{CO_2}, as an auxilliary supplier of CO_2 tc the blood. Were this to be substantiated

TABLE VI. Effects of Varying V_D at Constant V_T[a] on P_{O_2} and P_{CO_2} Values Leaving the Lung

V_D (ml)	V_{FA} (ml)	$F_{E_{O_2}}$	$F_{E_{CO_2}}$	$P_{E_{O_2}}$ (mm Hg)	$P_{E_{CO_2}}$ (mm Hg)
0.7	12.5	0.157	0.042	111	29.9
1.7	11.5	0.153	0.046	108	32.5
2.7	10.5	0.147	0.051	104	35.7
3.7	9.5	0.142	0.056	100	39.1
4.7	8.5	0.133	0.062	94	43.9
5.7	7.5	0.123	0.070	87	49.6
6.7	6.5	0.110	0.081	78	57.3

[a] V_T = 13.2 ml.

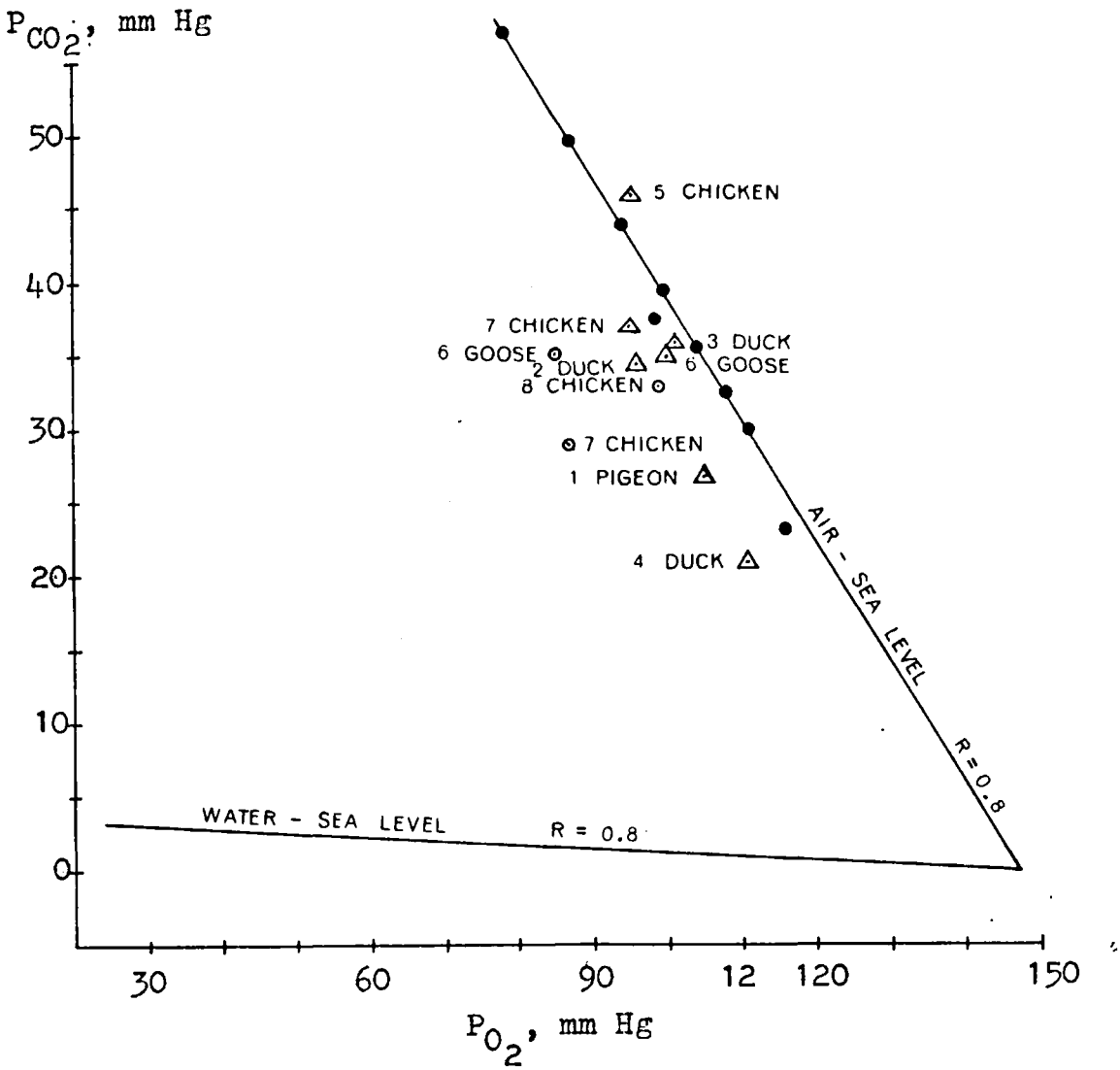

Figure 8. Comparison of Avian End Tidal and Arterial Blood Gases at Sea Level.

△ end tidal gases, ⊙ arterial blood gases, ● calculated end tidal values for varying Vp. Data from Lasiewski 1972 [citing (1), (4) Soum 1896; (2) Dotterweich 1933; (3) Vos 1935 and (5) Graham 1939]; (6) Cohn and Shannon 1968; (7) Piiper, Drees and Scheid 1970; and (8) Chiodi and Terman 1965. Water isoaltitude line from Rahn 1966.

it would be an effective means of avoiding the limitation of air breathing during hyperventilation.

The isoaltitude line for water at sea level with R = 0.8 is included in Figure 8 to show the effects of a different "inspired" medium. The low position of the water isoaltitude line is mostly due to the high solubility of carbon dioxide in water. As for air medium, increased ventilation to obtain a higher P_{O_2} results in lowered P_{CO_2}.

CONCLUSIONS

Birds exposed to simulated high altitude respond in a manner similar to mammals. As inspired P_{O_2} decreased, $P_{a_{O_2}}$ decreased and hyperventilation occurred. The resulting washout of CO_2 indicated that birds have no special means of preserving CO_2 under these conditions.

The increased functional capacity of birds over mammals at altitude is probably not due to their unique respiratory system since it does not provide better oxygenation of the blood. The explanation may lie in an increased circulatory response which would bring more blood and therefore more O_2 to the tissues or in better extraction of O_2 by the tissues. Tucker's analysis (1968) suggests this may be true, but direct measurements are needed.

APPENDIX I

SAMPLE CALCULATIONS FOR ISOALTITUDE LINES

Alveolar venitlation equation of Fenn, Rahn, and Otis (1946):

$$P_{A_{O_2}} = P_{I_{O_2}} + \frac{P_{A_{CO_2}} F_{I_{O_2}} (1 - R)}{R} - \frac{P_{A_{CO_2}}}{R}$$

Calculation of isoaltitude lines for graph:

Intercept

For $P_{A_{CO_2}} = 0$, $P_{A_{O_2}} = P_{I_{O_2}}$ regardless of R.

Other points

Assume R = 0.8

altitude, m	$P_{I_{O_2}}$	$F_{I_{O_2}}$	$P_{A_{CO_2}}$	$P_{A_{O_2}}$
2500	105.5	0.164	25	75.3

$$P_{A_{O_2}} = 105.5 + \frac{(25)(0.164)(0.2)}{0.8} - \frac{25}{0.8}$$

$$= 75.3 \text{ mm Hg}$$

LIST OF SYMBOLS

I used abbreviations to conform to the standard symbols of respiration physiology (Comroe et al. 1950, Dejours 1966).

V	gas volume
$\dot{V}$	gas volume per unit time
P	gas pressure in general
F	fractional concentration in dry gas
f	respiratory frequency (breaths per minute)
R	respiratory exchange ratio
BTPS	body temperature, pressure, saturated with water

Subscript:

I	inspired gas
E	expired gas
A	alveolar gas
T	tidal gas
D	dead space gas
B	barometric
a	arterial

Example:

V_T	tidal volume
$\dot{V}_{O_2}$	consumption of oxygen

$F_{I_{CO_2}}$ fractional concentration of CO_2 in inspired dry gas

$P_{a_{O_2}} - P_{E_{O_2}}$ difference of the partial pressures of oxygen between arterial blood and expired gas

In addition from Calder (1968):

f_h cardiac frequency (beats per minute)

Also subscript FA is gas in fresh air.

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