CARDIOPULMONARY RESPONSES TO EXERCISE IN THE DUCK

by

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GENERAL INTRODUCTION

Throughout history, numerous studies have been directly or indirectly related to exercise physiology. In the 1800's Schwann, the co-founder of the cell theory, was the first to measure the respiratory quotient on an exercising man. In 1890, Zuntz made a great technological advance in exercise physiology when he introduced the non-rebreathing valve, then continued his work on exercise by being the first to utilize a treadmill to study exercise in horses. During the 20th century, exercise physiology gained more support with pioneers such as Hill, Krogh, and Meyerhoff, who received the Nobel prize for their work.

Exercise physiology, in a general sense, attempts to explain how the living organism functions under conditions which tax the upper limits of its physical performance. By increasing work intensities, one can get a greater understanding of not only the mechanisms which govern the body systems at rest, but also gain insight into how these systems operate during exercise. Barcroft[1] stated that, "the condition of exercise is not a mere variant of the condition of rest, it is the essence of the machine." He was impressed by the "majesty" of the locomotive standing "by the platform of a railway station," but to understand the function of the locomotive it was necessary to study it during its maximal activity.

The purpose of investigating the cardiopulmonary response to exercise in birds was to determine if the conventional theories, regarding the mechanisms which control ventilation and hemodynamics during rest, could

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[1] J. Barcroft, Features in the architecture of physiological function. University Press, Cambridge. pp. 1-368, 1934.

explain the responses elicited by the animal during exercise. It is the attempt of this thesis to add to the already vast quantity of information concerning the factor(s) responsible for the control of ventilation during exercise.

PART I. ARTERIAL AND MIXED VENOUS BLOOD GAS TENSIONS IN EXERCISING DUCKS

ABSTRACT

Adult White Pekin ducks were exercised at three work levels on a treadmill at speeds of 0.9, 1.47, and 2.16 km/hr for 20 minutes with a 90 minute rest period following each exercise period. Blood gas and pH analyses were performed on samples simultaneously withdrawn from the brachial artery and right ventricle (as an estimate of mixed venous blood) at predetermined intervals during the experiment. Both arterial and mixed venous PCO_2 significantly decreased with increases in the level of exercise. Arterial pH did not change significantly from resting values at any exercise level. Mixed venous pH decreased at the onset of exercise but returned to near resting values by the end of each exercise period. These measurements indicate that ducks increase their ventilation during exercise above that required to eliminate the generated CO_2. Because the increased ventilation produces a reduction in arterial PCO_2, it is unlikely that peripheral or central CO_2-sensitive chemoreceptors are responsible for the ventilatory drive.

INTRODUCTION

The majority of studies on blood gas tensions during exercise have been conducted on humans or other mammals. Information concerning the blood gas values in exercising birds is limited; however, two studies have been reported. Penguins, during unrestrained field exercise and treadmill walking, increased their arterial O_2 tension and O_2 saturation but did not appreciably change arterial pH until exercise was severe and exhausting (8). Pigeons, flying in a wind tunnel, exhibited a decrease in arterial and mixed venous PCO_2, a decrease in arterial and mixed venous pH, and a decrease in mixed venous PO_2; arterial PO_2 increased over resting values (2). In the present study, we report on arterial and mixed venous blood gas tensions and acid-base status during rest and during various levels of exercise in ducks.

METHODS

Animal preparation. Ten adult White Pekin ducks (*Anas platyrhynchos domesticus*) weighing 2.2-3.2 kg were obtained from a local breeder, housed on an indoor floor pen, and provided with feed and water *ad libitum*. Ducks were weighed, placed in dorsal recumbency, and administered 1.0-2.0 ml xylocaine (1% lidocaine HCl, Astra Pharmaceutical) subcutaneously on the ventral side of the right wing around the cutaneous ulnar vein and brachial artery. The brachial artery was cannulated using a polyethylene catheter (Clay Adams PE 90). Silastic tubing (Dow Corning, 0.76 mm ID, 1.65 mm OD) was inserted into the right ventricle via the cutaneous ulnar vein. Catheter position was verified at the end of the experiment.

Recordings. Arterial blood pressure and right ventricular pressure were measured with pressure transducers (Statham, model P23Gb and model

P23De) and recorded on a multichannel pen recorder (Brush, model 481). Hematocrit was determined on arterial blood samples by a microcentrifuge method (11).

A treadmill was fabricated from a belt sander. The treadmill belt provided a 152 mm by 610 mm silicone rubber-coated running surface and was driven by a variable-speed motor. A wire cage was constructed around the belt to confine the duck on the treadmill. Openings in the top of the cage enabled the catheters to extend to the sampling syringes, thus eliminating any handling of the animal throughout the experiment. The sides and back of the cage were draped so that the duck could not see anyone during the rest periods; this minimized the possibility of exciting visual stimuli.

The pH and PCO_2 of arterial and mixed venous blood were analyzed at 41.0° C with a blood gas analyzer (Instrumentation Laboratories, model 113). Body temperature of the duck was not measured because a rectal probe appeared to impede exercise, and therefore blood gas values were not corrected for temperature changes throughout exercise. The pH electrode was calibrated before and after each exercise period with buffers of pH 6.840 and 7.384. The PCO_2 electrode was calibrated with gases (5% CO_2, 15% O_2, and 80% nitrogen and 0% O_2, 10% CO_2, and 90% nitrogen) derived from gas mixing pumps (Wösthoff, model 301 a/F). The standard bicarbonate concentration was calculated with a blood gas calculator (10) using the pK' for carbonic acid and the solubility coefficient for CO_2 in avian plasma reported by Helbacka _et al_. (5).

Experimental protocol. Several days before an experiment, each duck was allowed one or two practice runs on the treadmill. This served to (a) accustom each duck to running on the treadmill and (b) determine the maximum running speed the ducks could successfully endure for 20 min.

Maximum running speed was found to be 2.16 km/hr; only ducks which successfully met this criterion were used. Conversely, the slowest walking speed at which the ducks would continue to exercise was 0.9 km/hr.

Three predetermined, randomly ordered treadmill speeds (0.9, 1.47, and 2.16 km/hr) at a treadmill incline of 3° constituted the exercise levels of each experiment. Each 20 min exercise period was followed by a 90 min rest period. Samples of arterial and mixed venous blood (about 1.5 ml) were anaerobically withdrawn at four predetermined time intervals during rest and exercise and immediately analyzed for pH and PCO_2. Catheters were flushed with approximately 0.6 ml of saline between samples. Blood taken from donor ducks prior to experimentation was kept tonometered with gas (5% CO_2, 15% O_2, and 80% N_2) throughout, and was used to replace blood withdrawn from the exercising birds. To prevent coagulation, 500 IU of heparin (Organon, Inc.) was added to 50 ml of tonometered blood. No adverse signs resulted from blood transfusions.

An additional experiment was performed on one duck to test the possible influence of cardiac catheterization on the action of the heart. A polyethylene catheter was placed in the right brachial artery under local anesthesia for measuring arterial pH and PCO_2, but the right ventricle was not catheterized. Exercise was conducted as previously described.

Data analysis. The data were analyzed on an ITEL AS/5-3 computer using a two-way analysis of variance to test for difference among means. The means were separated using the least square differences. The level of probability at which means were considered to be significantly different was $P \leq 0.05$.

RESULTS AND DISCUSSION

Table 1 compares hemodynamic variables during rest before the experiment began and 90 min after the last exercise period. The mean arterial blood pressure, right ventricular pressure, systolic and diastolic blood pressures did not indicate any deterioration of the animal's cardiovascular status from the start to the finish of the experiment. Although there was a statistically significant drop in hematocrit over the course of the experiment, this did not appear to have any noticeable effect on the cardiovascular pressures. The fall in hematocrit may have been due to hemodilution resulting from repeated flushing of the catheters with saline after each sample was taken.

Figure 1 illustrates the average blood gas values during rest and significant differences caused by exercise. Arterial ($PaCO_2$) and mixed venous PCO_2 ($P_{\bar{v}}CO_2$) declined from resting values of 31 torr and 34 torr, respectively, to 19.5 and 25.5 torr during maximal exercise. Although an elevation in body temperature of 2 to 3° C during exercise--a value estimated from the findings of Taylor _et al._ (12) and Butler _et al._ (2)--would result in PCO_2 values from 2 to 3 torr higher than those reported, the magnitude of the PCO_2 changes with exercise was sufficiently great so that significant reductions remained. Arterial pH, uncorrected for temperature, increased during exercise; however, arterial pH would not have increased above resting values if a correction for an increase in body temperature of 2 to 3° C had been applied. Mixed venous pH exhibited a sharp decline at the onset of exercise, the severity of the drop increasing with increasing treadmill speed, but characteristically rose to near resting values by the end of exercise. Arterial and mixed venous plasma bicarbonate concentration

TABLE 1. Cardiovascular variables in 10 White Pekin ducks before exercise and 90 minutes after the last exercise period.

Variable	Pre-experiment	Post-experiment
Mean Arterial Blood Pressure (mm Hg)	145 ± 5.5[a]	145 ± 5.0[a]
Systolic Blood Pressure (mm Hg)	201 ± 5.3	190 ± 7.1
Diastolic Blood Pressure (mm Hg)	117 ± 6.7	119 ± 9.7
Right Ventricular Pressure (mm Hg)	32 ± 2.6	27 ± 2.1
Hematocrit %	32.5 ± 1.4[b]	25.6 ± 0.8[b]

[a] Means ± standard error of the mean.

[b] Significantly different ($P \leq 0.05$).

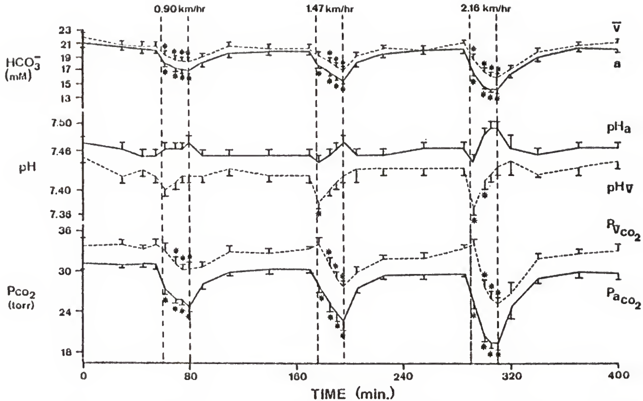

Fig. 1. Effect of exercise on arterial and mixed venous pH, PCO_2 and bicarbonate concentration in ten Pekin ducks. Mean $\pm$ standard error; * denotes significant difference from pre-exercise where $P \leq 0.05$.

declined approximately 5 mM at the two lowest exercise speeds, and 6 mM at the highest exercise speed. Although uncorrected for temperature, these data clearly illustrate how blood gas tensions and the acid-base status of the duck change during running.

The blood gas response to exercise when a duck ran without the cardiac catheter implanted remained the same as for ducks with the heart catheter in place. Therefore, the cannula in the right ventricle had no apparent adverse influence on heart action during exercise. No hemorrhage or myocardial damage was evident upon gross observation of the heart at necropsy, in the birds exercised with a heart catheter implanted.

The mean resting values of arterial pH, PCO_2, and bicarbonate concentration observed in the present study were similar to those reported by Calder and Schmidt-Nielsen (3) in nine different species of birds and by Kawashiro and Scheid (7) in undisturbed, awake ducks and chickens using a remote-control sampling device. Resting mixed venous blood gas tensions in our ducks were similar to those reported by Piiper _et al_.(9) in anesthetized chickens.

Our data indicate that ducks hyperventilate during exercise; arterial PCO_2 is reduced by as much as 10 torr during severe exercise. The duck, therefore, increases its ventilation far in excess of its CO_2 production, as indicated also by the fall in mixed venous PCO_2. The hyperventilation during exercise cannot be explained by the altered discharge of known chemoreceptors in the bird. Carotid body chemoreceptors or those in the central nervous system are activated by elevated PCO_2 or decreases in arterial pH and arterial PO_2 (1, 6). In the running ducks, the arterial PCO_2 decreased and arterial pH remained unchanged; thus, these variables could not have provided the stimulus for the hyperventilation. Furthermore, intrapulmonary CO_2 receptors (4) should have increased their discharge frequency with lowered intrapulmonary CO_2 concentration and thereby inhibited ventilation.

Much of the information relating increases in ventilation to mechanoreceptor activity from exercising muscles is inconclusive. However, Tibes (13) observed that in exercising muscles of the dog the discharge of small group III and IV fibers elicits a strong ventilatory drive. It is possible that local metabolites from exercising muscles could provide the necessary stimulus to excite these nerve fibers in the duck and thus increase ventilation despite hypocapnia.

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PART II. RESPIRATORY AND CARDIOVASCULAR RESPONSE TO EXERCISE IN THE DUCK

ABSTRACT

To study ventilatory and cardiovascular responses of the duck to running, adult White Pekin ducks were exercised for 20 minutes on a treadmill (3° incline) at two speeds: 0.9 and 1.47 km/hr. Each exercise period was followed by a 90 minute rest period. Heart rate, systolic and diastolic blood pressure increased significantly during each exercise period. During exercise, tidal volume decreased and respiratory frequency increased. Minute ventilation increased at the onset of exercise and continued to increase throughout, while clavicular air sac PCO_2 decreased. Both arterial PCO_2 and mixed venous PCO_2 decreased as the running speed increased. Mixed venous pH decreased at the onset of exercise but returned to near resting values by the end of an exercise period. Arterial pH did not significantly change from control values at either exercise period. Arterial PO_2 exhibited significant increases at both exercise speeds, while arterial and mixed venous plasma bicarbonate concentration decreased significantly with each exercise period. Body temperature increased 1-2° C during each run. Because the increased ventilation produced a reduction in arterial PCO_2 it is unlikely that peripheral or central CO_2-sensitive chemoreceptors were responsible for the ventilatory drive but that drive may result from hyperthermia or activity of certain muscle afferents.

INTRODUCTION

Many studies have dealt with changes in blood gas tensions and ventilatory adjustments during exercise in humans and other mammals (9, 13, 33). However, the nature of the stimulus and the controlled variable(s) involved in the control of ventilation remain poorly understood. During moderate muscular exercise in mammals arterial PCO_2 ($PaCO_2$) and arterial pH (pHa) are regulated about control values despite increases in CO_2 production; $PaCO_2$ decreases only with very severe and exhaustive exercise (32).

The paucity of information on ventilation and blood gas tensions in exercising birds is due mainly to the difficulty in measuring these variables on an unrestrained bird. However, there have been two studies on blood gas changes and several studies on ventilatory changes during exercise. In the running penguin, PaO_2 and O_2 saturation increase but no appreciable change in pHa occurs until exercise is severe and exhaustive (23). Pigeons, during wind tunnel flight, exhibit a decrease in $PaCO_2$, $P_{\bar{v}}CO_2$ and $P_{\bar{v}}O_2$ in addition to decreases in pHa and $pH_{\bar{v}}$; PaO_2 increases over resting values (6). Respiratory frequency (fresp) increases during wind tunnel flight at least twofold in the budgerigar (30), starling (29), and crow (2), and up to 20 times resting values in the pigeon (6, 14, 19). Tidal volume (V_T) was found to increase two fold during flight in the fish crow (2), fourfold in the starling (29) and twofold during walking in the pigeon (14). However, during flight in the pigeon there was little increase in V_T, but a 20 fold increase in ventilation resulting mainly from the increased rate of breathing; V_T decreased only when the birds were panting (14). PCO_2 falls and PO_2 rises in the anterior thoracic air sac of the starling during flight suggesting these birds hyperventilate (29).

In the present study, we measured arterial and mixed venous blood gas tensions, ventilation, clavicular air sac gas concentrations and body temperature during rest and various levels of running in ducks, in an attempt to define the variable(s) controlling ventilation during exercise.

METHODS

Animal preparation. Ten adult White Pekin ducks (*Anas platyrhynchos domesticus*) weighing between 2.2 and 3.4 kg (mean, 2.7 kg) were obtained from a local breeder, housed in an indoor floor pen and provided with feed and water *ad libitum*. The ducks were weighed, placed in dorsal recumbency, and administered a total dose of approximately 1.5 ml of a local anesthetic (2% lidocaine HCl with epinephrine, Astra Pharmaceutical) subcutaneously in three areas: a) ventral surface of the right wing around the cutaneous ulnar vein and brachial artery; b) around the anal orifice for insertion of a rectal probe for measuring body temperature (Yellow Springs Inst., model 401 and 44TD); and c) on the mid-ventral side of the neck at approximately the level of the 10th cervical vertebrae.

The brachial artery was cannulated using a polyethylene catheter (Clay Adams PE 90). Silastic tubing (Dow Corning, 0.76 mm ID, 1.65 mm OD) was inserted into the right ventricle via the cutaneous ulnar vein. Catheter position was verified at the end of the experiment. An incision was made on the mid-ventral side of the neck and the trachea was isolated and cannulated. A pneumotachograph (Fleisch, #0) was attached to the tracheal cannula and secured to the neck. Each duck was then administered Pentazocine (0.30 mg/kg body weight, Talwin-V, Winthrop Laboratories), a non-narcotic analgesic drug, intramuscularly following surgery to provide relief for any discomfort.

Recordings. Arterial blood pressure (from the cannulated brachial artery) and right ventricular pressure were recorded with pressure transducers (Statham, model P23Gb and P23De) on a multi-channel pen recorder (Brush, model 481). Heart rate was obtained from the arterial blood pressure tracing. Hematocrit was determined on arterial blood by a micro-centrifuge method (27). Ventilation was measured using a pneumotachograph (Statham-Godart, type 17212) and recorded on the pen recorder. The pneumotachograph was calibrated with a respiratory pump (Harvard Apparatus, model 681) before and after each experiment.

A treadmill was constructed from a commercial belt sander. The treadmill belt provided a silicone rubber-coated running surface which was driven by a variable speed motor. Speed of the belt was measured by computing the time interval between successive interruptions of a light beam by a slotted disc on the treadmill belt using an 8080 based microprocessor. A wire cage was constructed around the belt to confine the duck on the treadmill. Openings were cut in the top of the cage to enable the catheters to extend to the sampling syringes, thus eliminating any handling of the animal throughout the experiment. A television camera (Cohu, model 2810) mounted approximately 1 meter in front of the cage allowed continuous observation of the duck without its knowledge. The sides and back of the cage were draped to minimize visual stimuli to the duck. A constant background of white noise was generated using a preamplifier and an audio monitor (Grass P-511 and AM-8).

The pH, PCO_2 and PO_2 of arterial and mixed venous blood were analyzed at 41.0° C with a blood gas analyzer (Instrumentation Laboratories, model 113), and corrected to the body temperature of the bird (26). The pH electrode was calibrated before and after each exercise period with buffers of pH 6.840 and 7.384. The PCO_2 and PO_2 electrodes were calibrated with gases (5% CO_2, 15% O_2 and 80% N_2; and 0% O_2, 10% CO_2, and 90% N_2) derived from two gas mixing pumps (Wösthoff, model 301 a/F). A PO_2 electrode correction factor was determined from an equilibrated sample of the ducks' blood at the start of each experiment (24). The standard plasma bicarbonate concentration was calculated with a blood gas calculator (26), using the pK' for carbonic acid and the solubility coefficient for CO_2 in avian plasma (15).

<u>Experimental protocol</u>. The fastest treadmill speed at which all ducks could successfully run for 20 minutes was 1.47 km/hr. Conversely, the slowest walking speed at which they would continue to exercise was 0.9 km/hr. Exercise consisted, therefore, of these two speeds with the treadmill inclined at 3 degrees. Each exercise period was 20 minutes long and was followed by a 90 minute rest period. Samples (about 1.5 ml) of arterial and mixed venous blood were anaerobically withdrawn at four predetermined time intervals during each rest and exercise period, and immediately analyzed for pH, PCO_2 and PO_2. Catheters were flushed with approximately 0.6 ml of saline between samples. Blood taken from donor ducks was continuously tonometered (5% CO_2, 15% O_2 and 80% N_2) and was used to replace blood withdrawn during the experiment. To prevent coagulation, 500 IU of heparin (Organon, Inc.) was added to each 50 ml of tonometered donor blood. No adverse signs resulted from blood transfusions.

<u>Clavicular air sac gases</u>. Five adult Pekin ducks weighing between 1.5 to 2.1 kg (mean 1.8 kg) were prepared as described above but, in addition, a cannula was inserted into the clavicular air sac for measurement of clavicular air sac gas tensions. These ducks underwent the same exercise

protocol described above. The right ventricle was not cannulated and mixed venous blood gas tensions were not measured; the ducks' response to running without the right heart catheter was the same as when the heart catheter was in place.

Effects of low ambient temperature during exercise. An additional experiment was performed on one duck weighing 2.1 kg to test the effects of running at a reduced ambient temperature on changes in arterial blood gas tensions. The brachial artery was cannulated as previously described and the bird underwent the above mentioned protocol in a cold room at a temperature of 8.5° C.

Data analysis. The data were analyzed on an ITEL (model, AS/5-3) computer, using a two-way analysis of variance to test differences among means. The means were separated using the least square differences and the differences were considered significant at the 5% level of probability ($P \leq 0.05$). The asterisks (*) denote significant differences from pre-exercise to exercise periods only, and do not reflect changes in periods following each exercise level.

RESULTS

Cardiovascular changes during exercise. A comparison of cardiovascular variables before the birds were exercised and 90 minutes after the last exercise period is shown in Table 2. Only minor changes in heart rate, mean arterial pressure, right ventricular pressure, systolic and diastolic pressures, or in hematocrit occurred. The ducks' condition did not deteriorate from the start to the completion of the experiment and therefore changes observed with exercise were not influenced by failing condition of the animal.

TABLE 2. Cardiovascular variables in ten Pekin ducks measured before exercise and at the end of the experiment.

Variable	Pre-experiment	Post-experiment
Heart Rate (beats·min^{-1})	*231 ± 17.4	266 ± 21.8
Mean Arterial Blood Pressure (mm Hg)	118 ± 8.1	119 ± 5.6
Systolic Blood Pressure (mm Hg)	194 ± 6.3	175 ± 4.1
Diastolic Blood Pressure (mm Hg)	112 ± 11.1	107 ± 7.9
Right Ventricular Pressure (mm Hg)	**24.5 ± 2.2	21.4 ± 2.1
Hematocrit %	35.5 ± 1.8	31.1 ± 1.3

*Values are means ± standard error.

**The pre-experiment right ventricular pressure was measured with the birds restrained and in a supine position.

The cardiovascular changes, with significant differences from rest, that occurred during the two exercise periods are shown in Figure 2. Heart rate increased approximately 90% over resting values at both exercise speeds, the increase related to the intensity of exercise. Calculated mean arterial blood pressure rose 30% and systolic and diastolic pressures increased approximately 20% and 40%, respectively, above resting values regardless of treadmill speed.

Ventilatory response to exercise. At the onset of either level of exercise, minute volume rapidly increased within the first two minutes and continued to rise at a slower rate until the completion of the exercise period (Fig. 3). Ventilation was highest at the fastest treadmill speed. Respiratory frequency also rose sharply at the onset of exercise and the magnitude of the increase was slightly higher at the faster treadmill speed. Tidal volume decreased at the onset of exercise from 90 ml at rest to 26 ml by the end of an exercise period. Tidal volume did not show any relationship to the degree of exercise, the fall being the same at both exercise speeds.

Blood gas changes with exercise. Figure 4 illustrates the average blood gas values and significant differences from rest to exercise. Arterial PCO_2 declined from 25.1 torr at rest to 18.7 torr during the fastest exercise speed. Mixed venous PCO_2, on the other hand, rose significantly by 2 torr at the onset of exercise then fell to 25 torr during the highest work rate. Mixed venous pH initially exhibited a sharp decline at the beginning of exercise but rose to near resting values by the end of exercise; arterial pH did not significantly change at either high or low treadmill speeds. Arterial and mixed venous plasma bicarbonate concentration

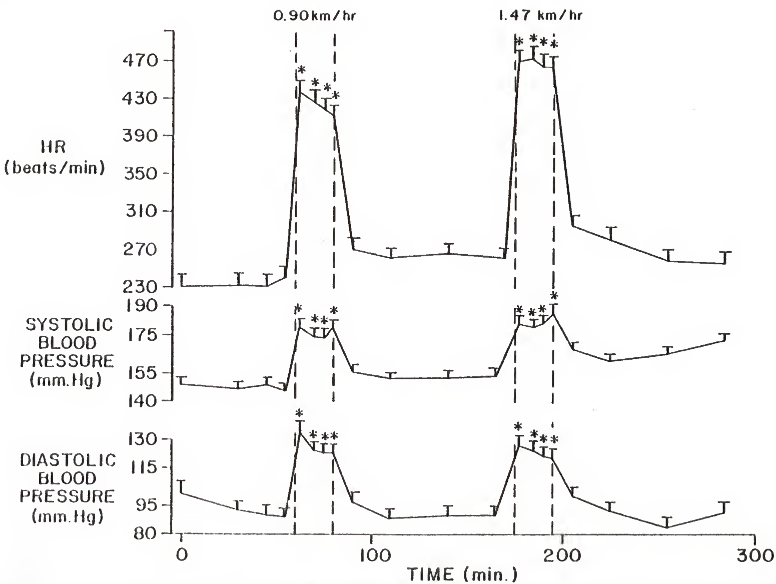

Fig. 2. Cardiovascular changes associated with two levels of exercise in ten Pekin ducks. Mean $\pm$ standard error; * denotes significant difference from pre-exercise ($P \leq 0.05$).

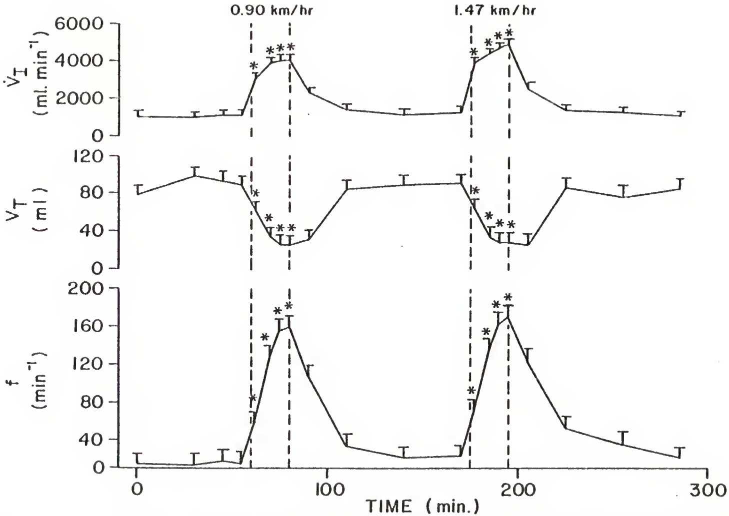

Fig. 3. Effect of exercise on ventilation in ten Pekin ducks. Mean $\pm$ standard error; * denotes significant difference from pre-exercise where $P \leq 0.05$.

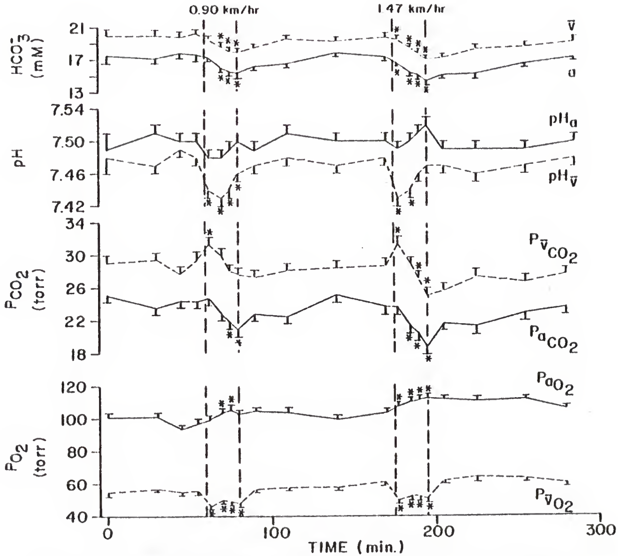

Fig. 4. Changes in arterial and mixed venous blood gas tensions, pH and plasma bicarbonate concentration in ten Pekin ducks. Mean $\pm$ standard error; * denotes significant difference from pre-exercise where $P \leq 0.05$.

declined at both treadmill speeds as the ducks exercised. Arterial PO_2 increased by 6 torr over resting levels at low exercise and by 15 torr during the fastest exercise speed, while mixed venous PO_2 declined during both periods of running.

<u>Body temperature changes with exercise</u>. Body temperature increased over the entire course of the experiment (Fig. 5). During exercise rectal temperature rose from 41.0° C at rest to 42.4° C at the low running speed; then during the rest period following exercise returned to a level approximately 0.8° C higher than the starting temperature. At the faster treadmill speed, rectal temperature rose from 41.8° C during rest to 43.2° C before completion of exercise. The total rise in body temperature from the start, prior to any exercise, to the completion of the last exercise period was on the order of 2.2° C.

<u>Clavicular air sac gas changes with exercise</u>. Clavicular air sac PCO_2 significantly decreased from a mean resting value of 37 torr to 27 torr at the highest exercise speed in the five ducks tested (Fig. 6). $PaCO_2$ of these birds decreased from 30 torr at rest to 24 torr at the end of the exercise period. Arterial pH again remained unchanged from rest to exercise and PaO_2 rose significantly by 10 torr at the fastest exercise speed. These blood gas changes were similar to that exhibited by the 10 ducks previously discussed.

<u>Response to exercise at low ambient temperature</u>. Rectal temperature increased by only 0.6° C in one duck running at 0.9 and 1.47 km/hr for 20 min at an ambient temperature of 8.5° C, and its body temperature returned to the resting value of 41.0° C. Arterial PCO_2 declined in this bird from 29 torr at rest to 19 torr, running at a speed of 1.47 km/hr. Arterial pH exhibited no change at the low exercise level but significantly increased

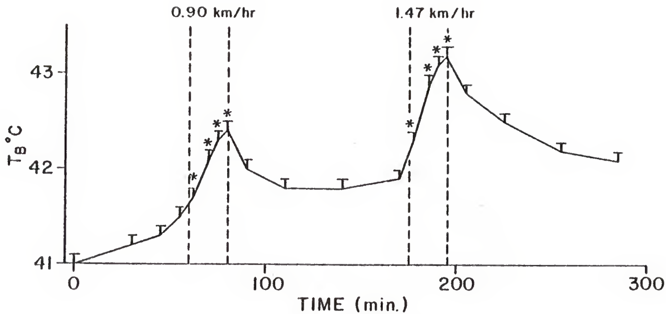

Fig. 5. Influence of exercise on rectal temperature in ten Pekin ducks. Mean $\pm$ standard error; * denotes significant difference from pre-exercise where $P \leq 0.05$.

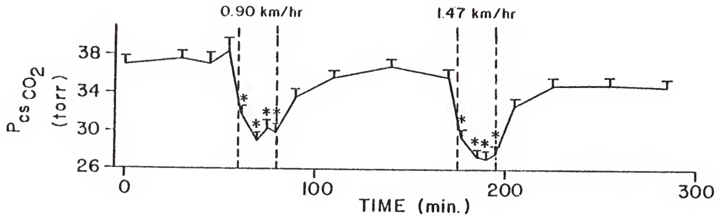

Fig. 6. Clavicular air sac PCO_2 during rest and two periods of exercise in five Pekin ducks. Mean $\pm$ standard error; * denotes significant difference from pre-exercise where $P \leq 0.05$.

by 0.07 pH units during the high exercise level, while arterial PO_2 increased from 97 torr at rest to 104 torr and 114 torr by the end of the low and high exercise levels, respectively. The blood gas response was dramatic during exercise in the cold environment much the same as in the duck that ran at an ambient temperature of 25° C; however, pHa rose during the high level of exercise in the cold, a response which was not observed in running ducks at 25° C.

DISCUSSION

Critique of methods. Tidal volume measurements during exercise in birds are difficult to obtain. We initially attempted to use a mask for this measurement but the ducks failed to run. We therefore were forced to cannulate the trachea mid-cervically under local anesthesia and secure a pneumotachograph to the neck. That most likely altered the normal humidifying and filtering of inspired air, the upper respiratory dead space volume, and airway resistance. The mean resting values of tidal volume, respiratory frequency and minute ventilation observed in the present study are slightly higher than those reported in unanesthetized, resting Pekin ducks (4, 5). These, or other unknown problems, resulting from the tracheal cannulation, presumably caused a lower $PaCO_2$ than expected for intact, resting ducks (17). Resting mixed venous PCO_2 averaged 10 torr lower and $P_{\bar{v}}O_2$ was approximately 14 torr higher than those reported for anesthetized chickens (25); however, the blood gas changes with exercise were large and clearly illustrated the ventilatory and acid-base response to this activity.

It was crucial to obtain resting blood gas and ventilatory values which were not affected by possible visual or auditory stimuli that would have adversely influenced breathing. We used a white noise generator and a video camera during the experiments to minimize such stimuli; these generally prevented irregular breathing, especially during rest.

The blood gas and pH values were corrected for body temperature changes of the ducks during exercise using temperature correction factors derived from mammalian blood (26). However, after completing these experiments, it became apparent that correcting blood gas and pH data for rectal temperature changes using mammalian correction factors may not be entirely precise. Therefore, duplicate 2 ml samples of duck blood, obtained by cardiac puncture, were adjusted to a pH of 7.50 with 1M $NaHCO_3$ and equilibrated for 20 min with gases (5% CO_2, 15% O_2 and 80% N_2) at temperatures from 41.0° C to 45.0° C. The PCO_2 and pH of the equilibrated blood were measured at 1° temperature increments with the blood gas analyzer at 41.0° C. From experiments on four ducks PCO_2 increased linearly with increasing temperature. Table 3 provides a comparison of PCO_2 temperature corrections for avian blood and those derived for mammalian blood (26). For temperatures less than 43° C the mammalian and avian correction factors are in close agreement; however for higher temperatures the Severinghaus correction factors underestimate the true PCO_2 by as much as 1.6 torr at 45° C. If we assume that the blood temperature did not increase above 44° C during exercise (which is likely because this is approaching the lethal temperature for birds (20)), the Severinghaus correction factor which we used would not cause significant error.

The levels of exercise were chosen based on preliminary observations that the maximum running speed which most intact ducks could successfully endure for 20 minutes was 2.16 km/hr. Conversely, the slowest walking speed at which they would continue to exercise was 0.9 km/hr. Birds with

TABLE 3. Avian and mammalian temperature correction factors for PCO_2*.

Avian PCO_2 correction			Mammalian PCO_2 correction (26)		
Temp. ^oC	ΔT	Ratio $(\frac{P\ cool}{P\ warm})$	Temp. ^oC	ΔT	Ratio $(\frac{P\ cool}{P\ warm})$
41	0.0	1.00	41	0.0	1.00
42	1.0	0.958	42	1.0	0.958
43	2.0	0.904	43	2.0	0.918
44	3.0	0.852	44	3.0	0.880
45	4.0	0.795	45	4.0	0.843

*Temperature corrections for PCO_2; these charts allow calculation of PCO_2 when temperature is changed anaerobically. To use this chart: PCO_2 measured at 41.0° C is corrected to 43.0° C body temperature by dividing the measured PCO_2 by .904 for birds and .918 for mammals or measured at 43° C and corrected to 41° C by multiplying by .904 and .918 for birds and mammals, respectively.

a cannulated trachea could not attain the maximum running speed; therefore the highest level of exercise used was an intermediate value between their maximum running capability and a slow walk.

Cardiovascular changes from rest to exercise. The abrupt rise in heart rate and blood pressure at the onset of exercise in running ducks and penguins (23), as well as flying birds (6, 14), is similar to mammalian cardiovascular changes during exercise (18). In mammals there have been many controversial attempts to explain the changes in cardiac output at the onset of exercise with ventilation. Initially, these changes were thought to be induced neurogenically because of their rapidity (9) perhaps as a result of increase in sympathetic discharge. However, it has been demonstrated that at the onset of exercise the flow of CO_2 from the mixed venous blood to the lungs quickly rises; this may be attributed to an immediate rise in cardiac output followed by an increased $P_{\bar{v}}CO_2$; this increased flow is sensed by receptors, possibly in the lung, which then increase ventilation to match the increased CO_2 flow and cardiac output (33).

The increase in cardiac output during exercise has been shown to be related mainly to an increase in heart rate, while stroke volume remains close to resting levels (9). In the running duck, heart rate increased two fold; thus, we can infer that cardiac output increased proportionally. Mean arterial pressure, on the other hand, increased only approximately 1.2 times during exercise; total peripheral resistance, the ratio of mean arterial pressure to cardiac output, must therefore have decreased during exercise, allowing the heart to pump more blood with higher efficiency than if peripheral resistance had remained unchanged. That response may have been facilitated by skin vasodilation as body temperature increased with exercise. These findings are similar to those of flying pigeons (6).

Ventilatory and blood gas changes from rest to exercise in birds. Our data indicate that ducks hyperventilate during exercise with respect to their CO_2 production. Respiratory frequency increased 10 times the resting levels while tidal volume decreased by 1.5 times resulting in a 4-5 fold increase in minute ventilation. As a result of the increased minute ventilation, PCO_2 was reduced by as much as 7 torr during the high level of exercise. Based on the increase in $\dot{V}_I$ and the fall in $PaCO_2$ there is a strong indication that the effective parabronchial ventilation, the volume of fresh gas that passes over gas exchange surfaces, increases sharply during exercise. During flight in the starling (29), pigeon (14), and fish crow (2), both respiratory frequency and tidal volume increase with an accompanying rise in ventilation. Upon completion of flight, a sharp fall in respiratory frequency and tidal volume account for the ensuing decline in ventilation. In the running duck, there is also an abrupt fall in ventilation at the completion of exercise, with respiratory frequency and tidal volume returning to resting levels; however, after completion of the high level of exercise, tidal volume continued to decrease for nearly 10 min before returning to pre-exercise values. Arterial pH underwent no significant change from rest to exercise in running ducks, despite the fall in $PaCO_2$, a finding in agreement with that of Millard et al. (23) on walking penguins.

The significant fall in clavicular air sac PCO_2 further indicates that the running duck hyperventilates. This measurement is indicative of a fall in parabronchial CO_2 concentration. Clavicular air sac PCO_2 has been shown to approximate end-expired PCO_2 (3). That clavicular air sac PCO_2, and presumably end-expired PCO_2 exceeded arterial PCO_2 is not atypical in birds, as explained by the cross current system for gas exchange (8, 22).

Possible receptors responsible for hyperventilation. Birds possess intrapulmonary CO_2 receptors; neural discharge from these receptors increases as airway CO_2 concentration decreases (10). Impulses from these receptors act centrally to inhibit ventilation. Thus, hyperventilation during exercise with ensuing reduction in intrapulmonary CO_2 concentration should have caused these receptors to increase their discharge frequency and thereby inhibit ventilation. It appears that these receptors are not driving ventilation during exercise; however, they may act to limit hyperventilation and thereby prevent arterial PCO_2 from falling to intolerable levels.

Other chemoreceptors, such as carotid bodies or those in the central nervous system, are activated by elevated PCO_2, reduced PO_2, or decreased pHa (16). During exercise, the stimuli to these receptors are reduced. Therefore, these chemoreceptors do not appear to be responsible for the hyperventilation accompanying exercise.

In our running ducks, body temperature rose by approximately 2° C during exercise, a finding common to other running or flying birds (6, 28). The rise in body temperature may have stimulated ventilation and the role of thermoreceptors may be important in the accompanying hyperventilation. In man, hyperthermia greater than 1° C leads to hyperventilation and hypocapnia (12). However, increased body temperature alone does not appear to be an independent stimulus in man; in moderate exercise, ventilation becomes stable after several minutes of exercise yet body temperature continues to rise (34). In addition, our experiment performed on a running duck at a lowered ambient temperature (8.5° C), indicates ventilation still increases and $PaCO_2$ decreases despite only a 0.6° C increase in body temperature. Those data suggest that thermoreceptors may not be causing the increased ventilation during exercise. Most birds that undergo heat stress exhibit a rise in body temperature with ensuing hypocapnia and alkalosis (11, 20, 21), although during moderate heat loads the duck is able to increase its ventilation without alkalosis or hypocapnia (4).

Neural input from muscles and joints is thought to cause the cardiovascular and ventilatory responses during passive movement of these structures in cats (1). Although these studies implicate mechanoreceptors from exercising muscles, other studies (7) suggest that the exercise hyperpnea in man is linked to metabolism through CO_2 production and that the relationship between ventilation and CO_2 production is the same regardless of the rate of limb movement (7). Tibes (31), has provided convincing evidence that discharge of small, unmyelinated, group III or IV afferent fibers from exercising muscles of the dog elicits a strong ventilatory drive. It is likely that local metabolites from exercising muscles could provide a sufficient stimulus to excite these small nerve fiber endings in the running duck and thereby increase ventilation, heart rate and blood pressure despite the hypocapnia that accompanies the exercise.

In summary, the hyperventilation associated with muscular exercise in the duck cannot be explained by stimulation of peripheral or central chemoreceptors bathed by arterial blood, but may result from an increased hyperthermic drive or the activity of certain muscle afferents responding to increases in blood flow, chemical stimulation, or increases in muscle temperature. Any combination of neurogenic or myogenic drives may provide information required for the ventilatory and cardiovascular adjustments during muscular exercise in the duck.

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DEDICATION

I dedicate this work to my father, the late James P. Kiley, Jr., whose respect for the value of an education has provided me with the encouragement and strength to continue my pursuit of higher education.

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APPENDIX TABLE I

EXPERIMENT I. UNCORRECTED ARTERIAL AND MIXED VENOUS PCO_2 (torr)

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

TIME (MIN)

Bird No.		Control 0	Control 30	Control 45	Control 55	Ex I 2	Ex I 10	Ex I 15	Ex I 20	Rest 10	Rest 30	Rest 60	Rest 90
1	Arterial PCO_2	30.8	29.9	11.0	29.9	27.5	26.3	26.4	26.0	29.0	29.8	31.8	31.1
	Mixed Venous PCO_2	29.6	33.0	32.7	33.0	33.2	32.5	31.8	32.4	33.5	34.9	32.2	34.2
2	Arterial PCO_2	36.7	33.0	11.0	32.9	30.9	29.0	28.6	27.8	31.0	32.8	36.3	33.0
	Mixed Venous PCO_2	36.5	38.1	34.4	39.0	39.5	38.0	35.5	36.9	33.5	37.8	37.6	34.3
3	Arterial PCO_2	27.4	29.7	27.8	30 6	26.2	23.4	--	21.3	24.1	29.1	30.6	30.1
	Mixed Venous PCO_2	39.3	32.2	33.4	33.1	37.3	27.4	26.9	25.8	28.5	34.1	34.7	33.0
4	Arterial PCO_2	31.6	30.5	33.0	30.4	27.2	26.8	27.9	27.6	29.5	29.4	31.3	29.2
	Mixed Venous PCO_2	30.8	33.5	13.7	35.5	30.4	32.4	32.0	32.6	32.3	32.4	31.0	31.3
5	Arterial PCO_2	31.0	31.8	11 3	32.7	25 5	23.5	22.4	23.5	28.5	30.6	28.8	30.4
	Mixed Venous PCO_2	37.9	33.8	36.4	34.5	36.6	28.8	28.8	29.4	32.8	31.8	34.4	33.1
6	Arterial PCO_2	29.9	33.0	30.8	31.0	27.2	27.6	26.1	25.8	27.3	31.1	29.2	31.7
	Mixed Venous PCO_2	32.1	31.5	12.6	30.2	32.2	31.0	32.0	29.9	30.6	29.3	32.9	33.2
7	Arterial PCO_2	31 2	31.0	29.8	31.2	26.2	26.7	25.7	25.0	26.1	29.0	28.4	28.4
	Mixed Venous PCO_2	32.6	12.0	33.0	33.1	31.9	29.2	28.8	28.5	27.8	31.5	31.4	30.3
8	Arterial PCO_2	27.2	29.4	30.6	29.0	28.7	26.1	27.3	27.2	27.8	29.3	30.8	29.6
	Mixed Venous PCO_2	11.5	33.0	30.6	33.4	29.7	32.0	29.9	32.6	29.6	33.3	30.4	34.8
9	Arterial PCO_2	13.4	30.1	32.0	29.5	23.6	23.2	21.0	21.8	27.4	28.5	26.3	28.7
	Mixed Venous PCO_2	15.5	16.9	33.0	33 8	28.5	27.8	27.0	27.3	29.6	30.5	31.7	33.9
10	Arterial PCO_2	12.7	11.3	32.3	30.4	29.5	26.4	24.3	23.2	28.3	29.2	29.4	30.3
	Mixed Venous PCO_2	33.2	35.4	13.5	34.1	32.0	31.7	28.9	28.2	28.9	32.8	30.8	32.8
$\bar{X}$	Arterial PCO_2	11.2	31.0	31.2	30.8	27.3	25.9	25.7	24.8	28.1	29.9	30.3	30.3
	Mixed Venous PCO_2	33.9	13.9	33.3	34.0	31.1	31.1	30.3	30.4	30.7	33.0	32.7	33.3
SE	Arterial PCO_2	0.88	0.41	0.56	0.43	0.66	0.61	0.71	0.79	0.73	0.41	0.84	0.48
	Mixed Venous PCO_2	1.02	0.69	0.51	0.78	1.11	0.98	0.77	1.04	0.68	0.75	0.71	0.42

Bird No.		Ex II 2	Ex II 10	Ex II 15	Ex II 20	Rest 10	Rest 30	Rest 60	Rest 90	Ex III 2	Ex III 10	Ex III 15	Ex III 20	Rest 10	Rest 30	Rest 60	Rest 90
1	Arterial PCO_2	30.2	25.2	24.1	20.4	28.6	27.2	29.5	30.0	25.7	22.6	21.5	20.3	27.5	30.2	32.9	31.2
	Mixed Venous PCO_2	36.4	32.8	28.8	26.5	29.8	30.3	30.9	30.8	31.7	29.0	27.3	26.3	29.4	32.0	34.7	34.6
2	Arterial PCO_2	31.0	31.0	29.1	29.0	30.7	30.7	32.2	31.2	30.4	26.4	24.7	24.3	29.9	31.5	31.6	35.5
	Mixed Venous PCO_2	19.2	37.3	36.2	34.7	34.4	31.5	35.5	36.6	39.5	34.2	31.5	29.6	32.4	35.7	37.3	39.5
3	Arterial PCO_2	26.1	21.8	21.1	18.3	24.5	--	29.7	29.3	18.5	17.0	15.7	--	--	--	--	--
	Mixed Venous PCO_2	--	28.5	29.2	24.8	29.1	--	30.0	36.0	30.6	27.6	25.0	--	--	--	--	--
4	Arterial PCO_2	28.2	27.6	26.3	25.7	30.4	29.7	28.5	29.1	26.6	19.0	17.7	16.7	25.4	30.8	31.2	29.2
	Mixed Venous PCO_2	33.4	33.2	30.7	29.5	32.5	32.7	27.3	32.7	35.0	26.7	23.6	22.8	28.9	34.3	32.7	35.1
5	Arterial PCO_2	26.0	23.0	21.5	21.0	26.3	27.9	30.4	31.0	24.3	20.3	18.3	17.8	23.8	29.5	29.2	29.8
	Mixed Venous PCO_2	35.3	28.6	27.9	27.0	30.3	31.8	35.0	35.1	34.4	25.5	25.3	23.5	28.7	30.5	33.7	32.3
6	Arterial PCO_2	26.7	26.3	24.2	22.9	27.6	30.8	27.6	29.2	25.3	21.9	20.6	19.6	25.7	27.6	24.1	29.0
	Mixed Venous PCO_2	36.0	30.4	29.5	27.1	31.5	32.4	31.6	32.7	34.4	28.9	28.0	26.1	29.0	29.7	30.5	30.5
7	Arterial PCO_2	25.9	26.4	23.7	23.7	25.6	30.2	29.4	29.9	25.5	21.0	19.7	18.7	22.3	27.6	29.9	--
	Mixed Venous PCO_2	32.7	29.8	29.6	27.8	28.7	30.2	33.7	31.4	32.2	25.5	25.0	23.3	24.2	28.5	32.9	--
8	Arterial PCO_2	29.0	26.6	27.5	27.0	28.8	30.3	32.1	31.2	26.3	23.0	23.8	24.4	27.1	29.2	31.2	28.1
	Mixed Venous PCO_2	12.3	33.1	30.4	10.5	31.2	34.9	34.5	34.7	33.9	29.4	29.0	28.6	27.3	34.9	30.3	32.2
9	Arterial PCO_2	23.8	19.4	18.7	18.0	26.0	29.6	27.6	27.9	23.8	16.7	16.2	16.7	27.8	29.7	30.2	28.7
	Mixed Venous PCO_2	28.9	26.9	23.8	23.6	26.4	31.7	29.5	32.5	33.4	24.6	20.8	22.6	27.3	31.2	31.5	31.5
10	Arterial PCO_2	29.1	21.9	21.3	26.0	27.9	29.2	29.2	29.4	30.0	19.0	18.2	16.6	13.7	27.1	29.9	28.0
	Mixed Venous PCO_2	32.7	30.4	24.3	25.6	25.8	32.3	30.8	32.4	35.9	26.3	24.6	25.1	14.6	29.3	32.0	31.3
$\bar{X}$	Arterial PCO_2	27.6	25.1	23.8	22.6	27.6	29.5	29.6	29.8	25.7	20.7	19.6	19.5	24.6	29.2	30.2	29.9
	Mixed Venous PCO_2	34.1	31.1	29.0	27.7	30.0	32.0	32.1	33.5	34.1	27.8	26.0	25.3	26.9	32.0	12.8	33.4
SE	Arterial PCO_2	0.71	1.03	1.02	1.18	0.65	0.41	0.51	0.34	1.05	0.94	0.95	1.02	1.58	0.51	0.91	0.83
	Mixed Venous PCO_2	0.99	0.96	1.09	1.01	0.81	0.47	0.87	0.62	0.79	0.98	1.06	0.84	1.69	0.88	0.73	1.04

APPENDIX TABLE 2

EXPERIMENT 1. UNCORRECTED ARTERIAL AND MIXED VENOUS PO_2 (torr)
AT REST AND DURING EXERCISE
WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

TIME (MIN)

Subj No.		Control 0	Control 30	Control 45	Control 55	Ex I 2	Ex I 10	Ex I 15	Ex I 20	Rest 10	Rest 30	Rest 60	Rest 90
1	Arterial PO_2	110.3	102.8	98.1	102.8	97.2	96.9	98.1	97.5	99.8	102.8	110.4	96.3
	Mixed Venous PO_2	66.9	61.9	61.9	61.9	46.9	52.2	48.5	48.8	69.0	73.8	65.6	70.0
2	Arterial PO_2	103.9	104.0	109.8	97.8	102.4	96.1	98.8	96.3	97.6	99.4	103.7	103.0
	Mixed Venous PO_2	70.7	72.0	66.5	65.5	48.8	53.0	49.8	48.5	62.2	68.5	61.4	58.5
3	Arterial PO_2	94.1	98.8	97.6	95.4	97.3	105.5	----	96.1	97.0	94.9	103.0	103.9
	Mixed Venous PO_2	58.5	53.0	62.8	53.7	44.9	44.5	----	40.5	59.5	54.3	52.1	55.7
4	Arterial PO_2	105.2	94.3	107.4	99.1	89.0	88.8	88.8	81.9	88.7	90.2	89.6	76.8
	Mixed Venous PO_2	64.9	68.0	63.7	65.9	46.2	49.8	47.3	45.4	60.4	64.6	59.6	61.0
5	Arterial PO_2	102 9	108.5	98.7	102.3	104.8	111.4	103.5	101.4	100.6	109.1	93.4	99.4
	Mixed Venous PO_2	65.9	60.8	65.4	60.4	51.3	49.4	49.4	47.7	63 3	61.5	63.7	57.3
6	Arterial PO_2	92.1	115.4	101.5	104.1	90.9	99.0	92.4	94.2	95.5	106.4	97.8	110.6
	Mixed Venous PO_2	67.4	64.7	65.4	61.3	49.6	48.1	48.1	47.4	58.6	55.8	65.3	60.5
7	Arterial PO_2	95.7	103.9	96.1	103.5	90.9	98.8	88.8	89.9	89.3	92.6	87.4	97.7
	Mixed Venous PO_2	63.7	55.2	57.9	53.4	51.3	48.2	47.0	45.1	53.7	53.0	56.3	52.6
8	Arterial PO_2	92.4	89.3	95.7	90.9	89.4	84.8	87.0	82.9	92.1	84.0	90.7	83.5
	Mixed Venous PO_2	51.8	59.5	52.0	54.4	39.5	43.1	40.3	40.6	48.7	53.4	52.6	53.5
9	Arterial PO_2	93.3	88.4	98.4	93.0	90.7	83.1	86.2	82.0	89.7	80.9	91.0	83.4
	Mixed Venous PO_2	56.4	61.7	59.9	64.4	45.8	46.4	42.5	40.6	50.6	57.4	51.6	58.4
10	Arterial PO_2	92.8	88.2	99.6	91.3	88.0	84.9	87.8	83.1	92.7	90.6	101.2	90.4
	Mixed Venous PO_2	57.8	61 2	57.1	64.1	42.7	45.4	41.6	39.9	51.6	59.4	54.3	59.0
$\bar{X}$	Arterial PO_2	98.3	99.4	99.8	98.0	94.1	94.9	92.4	90.9	94.3	95.1	96.8	94.5
	Mixed Venous PO_2	62.7	62.0	61.3	60.5	46.7	48.0	45.7	44.5	57.8	60.4	58.5	58.7
SE	Arterial PO_2	2.09	2.92	1.43	1.72	1.89	2.98	2.08	2.41	1.39	2.94	2.39	3.78
	Mixed Venous PO_2	1.78	1.77	1.61	1.73	1.19	1.02	1.12	1.16	2.04	2.22	1.81	0.98

Subj No.		Exp. II 2	Exp. II 10	Exp. II 15	Exp. II 20	Rest 10	Rest 30	Rest 60	Rest 90	Ex III 2	Ex III 10	Ex III 15	Ex III 20	Rest 10	Rest 30	Rest 60	Rest 90
1	Arterial PO_2	103.5	88.1	90.4	89.0	97.5	93.8	105.0	107.2	96.9	92.5	94.1	94.0	98.8	102.2	95.7	102.5
	Mixed Venous PO_2	49.8	50.6	42.5	47.8	58.8	64.0	63.6	59.1	44.0	47.5	44.1	43.1	58.8	60.0	62.9	59.4
2	Arterial PO_2	91.7	95.1	84.1	82.7	83.5	99.8	96.3	96.1	94.1	95.2	94.0	94.5	96.6	92.4	93.3	96.6
	Mixed Venous PO_2	47.5	49.0	46.1	43.9	54.9	60.7	66.8	64.0	45.7	47.6	45.2	45.1	58.5	62.2	62.2	61.0
3	Arterial PO_2	92.9	98.8	89.3	90.9	93.3	----	98.4	95.1	107.1	101.2	97.2	----	----	----	----	----
	Mixed Venous PO_2	----	42.1	39.6	19.0	55.1	----	51.8	62.0	44.3	45.6	43.0	----	----	----	----	----
4	Arterial PO_2	90.4	89.0	91.5	90.2	95.1	91.5	81.7	87.6	98.4	95.0	97.0	93.7	97.4	94.1	101.2	92.7
	Mixed Venous PO_2	46.6	49.8	48.7	47.3	63.4	64.5	56.1	65.9	46.3	47.0	44.5	43.5	60.9	66.2	61.6	68.5
5	Arterial PO_2	94.1	102.5	92.7	96.3	93.3	99.0	89.9	94.9	96.3	104.2	97.2	97.2	94.7	95.6	93.7	101.3
	Mixed Venous PO_2	45.3	44.3	43.9	42.4	59.9	53.0	53.8	45.7	48.1	45.4	44.7	43.3	59.9	56.1	63.3	55.1
6	Arterial PO_2	99.7	108.7	101.4	105.1	104.1	111.3	102.8	111.5	98.1	108.5	99.7	101.4	98.3	103.3	100.9	105.1
	Mixed Venous PO_2	49.0	51.0	51.3	51.4	64.4	62.8	65.4	62.6	48.7	47.6	46.3	45.3	63.8	58.7	64.4	57.1
7	Arterial PO_2	95.0	99.4	90.9	91.5	88.8	100.2	90.0	100.6	96.3	99.0	88.9	90.2	88.8	94.8	90.0	-----
	Mixed Venous PO_2	49.1	47.2	46.2	44.0	52.4	54.8	59.5	54.8	42.7	43.2	41.1	40.2	51.1	49.1	57.7	-----
8	Arterial PO_2	90.7	84.0	85.7	78.8	93.0	82.4	95.3	85.1	100.6	92.1	93.0	87.0	96.5	88.4	90.7	83.7
	Mixed Venous PO_2	39.5	41.9	39.2	38.3	46.5	52.6	52.7	52.9	39.5	42.8	39.5	39.9	51.5	55.8	50.0	54.1
9	Arterial PO_2	93.6	89.9	91.2	88.4	91.1	88.0	93.3	84.2	98.4	94.6	94.9	88.8	89.7	82.8	99.8	87.9
	Mixed Venous PO_2	45.3	44.6	41.1	41.3	55.1	57.5	54.5	58.4	45.5	45.2	40.8	40.4	51.7	61.8	61.0	62.9
10	Arterial PO_2	85.5	84.2	86.7	84.0	76.5	91.3	104.2	94.0	87.3	89.9	91.0	85.8	99.8	92.5	101.2	90.0
	Mixed Venous PO_2	43.7	46.5	41.1	40.0	47.0	65.4	60.2	65.4	42.2	44.5	39.2	37.6	47.3	62.7	54.3	60.2
$\bar{X}$	Arterial PO_2	93.7	94.0	90.4	89.7	91.6	94.4	95.7	95.1	97.4	97.2	94.7	92.5	95.6	94.0	96.3	95.2
	Mixed Venous PO_2	46.2	46.7	44.0	43.5	55.8	59.5	58.4	59.1	44.7	45.6	42.8	42.0	55.9	59.2	59.7	59.8
SE	Arterial PO_2	1.58	2.61	1.51	2.33	2.39	3.20	2.32	2.64	1.57	2.03	1.10	1.68	1.30	2.10	1.53	2.68
	Mixed Venous PO_2	1.08	1.07	1.27	1.34	1.93	1.70	1.73	2.02	0.88	0.63	0.89	0.88	1.87	1.67	1.60	1.61

APPENDIX TABLE 3

EXPERIMENT I. UNCORRECTED ARTERIAL AND MIXED VENOUS pH

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

TIME (MIN)

Bird No.		Control 0	Control 30	Control 45	Control 55	Ex I 2	Ex I 10	Ex I 15	Ex I 20	Rest 10	Rest 30	Rest 60	Rest 90
1	Arterial pH	7.467	7.448	7.446	7.448	7.453	7.463	7.454	7.460	7.433	7.434	7.434	7.432
	Mixed Venous pH	7.445	7.429	7.424	7.429	7.408	7.408	7.423	7.405	7.410	7.394	7.415	7.405
2	Arterial pH	7.402	7.427	7.414	7.414	7.407	7.402	7.410	7.425	7.410	7.414	7.412	7.404
	Mixed Venous pH	7.389	7.380	7.380	7.382	7.343	7.367	7.372	7.365	7.391	7.394	7.380	7.375
3	Arterial pH	7.512	7.489	7.424	7.472	7.462	7.488	7.492	7.509	7.488	7.437	7.460	7.434
	Mixed Venous pH	7.510	7.423	7.467	7.442	7.384	7.420	7.441	7.455	7.455	7.530	7.423	7.417
4	Arterial pH	7.521	7.467	7.482	7.444	7.511	7.468	7.470	7.464	7.399	7.475	7.446	7.496
	Mixed Venous pH	7.488	7.446	7.443	7.429	7.462	7.440	7.431	7.427	7.420	7.414	7.459	7.440
5	Arterial pH	7.474	7.438	7.442	7.430	7.414	7.446	7.452	7.440	7.415	7.424	7.434	7.430
	Mixed Venous pH	7.434	7.412	7.410	7.411	7.355	7.407	7.402	7.397	7.388	7.390	7.406	7.409
6	Arterial pH	7.492	7.469	7.467	7.459	7.485	7.478	7.464	7.469	7.466	7.500	7.498	7.474
	Mixed Venous pH	7.495	7.455	7.440	7.450	7.437	7.432	7.424	7.428	7.446	7.462	7.475	7.435
7	Arterial pH	7.469	7.472	7.472	7.451	7.464	7.463	7.460	7.494	7.472	7.464	7.463	7.455
	Mixed Venous pH	7.440	7.446	7.431	7.425	7.409	7.414	7.421	7.434	7.441	7.438	7.412	7.424
8	Arterial pH	7.458	7.455	7.448	7.460	7.434	7.415	7.444	7.408	7.425	7.412	7.404	7.413
	Mixed Venous pH	7.433	7.413	7.420	7.420	7.394	7.373	7.363	7.366	7.403	7.384	7.388	7.361
9	Arterial pH	7.430	7.460	7.441	7.451	7.473	7.470	7.469	7.490	7.458	7.446	7.451	7.450
	Mixed Venous pH	7.414	7.422	7.406	7.405	7.400	7.397	7.418	7.430	7.435	7.415	7.426	7.416
10	Arterial pH	7.458	7.445	7.440	7.442	7.470	7.490	7.505	7.511	7.485	7.491	7.482	7.485
	Mixed Venous pH	7.419	7.408	7.408	7.412	7.431	7.439	7.457	7.454	7.455	7.463	7.463	7.469
$\bar{X}$	Arterial pH	7.470	7.457	7.448	7.447	7.457	7.458	7.462	7.467	7.445	7.450	7.448	7.447
	Mixed Venous pH	7.447	7.423	7.433	7.421	7.402	7.410	7.415	7.416	7.424	7.428	7.425	7.416
SE	Arterial pH	.010	.006	.007	.006	.010	.009	.008	.011	.010	.009	.009	.011
	Mixed Venous pH	.012	.007	.009	.007	.010	.008	.009	.010	.008	.015	.010	.011

Bird No.		Ex II 2	Ex II 10	Ex II 15	Ex II 20	Rest 10	Rest 30	Rest 60	Rest 90	Ex III 2	Ex III 10	Ex III 15	Ex III 20	Rest 10	Rest 30	Rest 60	Rest 90
1	Arterial pH	7.433	7.456	7.460	7.456	7.454	7.455	7.450	7.444	7.452	7.470	7.473	7.548	7.411	7.435	7.469	7.502
	Mixed Venous pH	7.378	7.401	7.414	7.418	7.426	7.491	7.429	7.437	7.396	7.412	7.409	7.410	7.413	7.424	7.469	7.460
2	Arterial pH	7.410	7.416	7.425	7.425	7.437	7.458	7.428	7.424	7.399	7.452	7.463	7.423	7.451	7.446	7.521	7.474
	Mixed Venous pH	7.356	7.355	7.374	7.381	7.416	7.404	7.413	7.393	7.340	7.382	7.388	7.405	7.421	7.420	7.436	7.441
3	Arterial pH	7.437	7.470	7.451	7.500	--	--	7.482	7.483	7.432	7.469	7.485	--	--	--	--	--
	Mixed Venous pH	7.381	7.393	7.398	7.433	7.422	--	7.422	7.450	7.338	7.375	7.420	--	--	--	--	--
4	Arterial pH	7.476	7.448	7.468	7.492	7.455	7.473	7.482	7.499	7.444	7.494	7.513	7.538	7.445	7.434	7.425	7.465
	Mixed Venous pH	7.426	7.415	7.416	7.439	7.550	7.438	7.478	7.469	7.375	7.452	7.457	7.483	7.410	7.399	7.392	7.454
5	Arterial pH	7.436	7.442	7.455	7.451	7.406	7.441	7.451	7.456	7.432	7.460	7.460	7.460	7.419	7.440	7.440	7.424
	Mixed Venous pH	7.370	7.397	7.410	7.410	7.384	7.419	7.420	7.422	7.371	7.403	7.409	7.405	7.389	7.415	7.403	7.413
6	Arterial pH	7.439	7.463	7.477	7.481	7.458	7.459	7.499	7.489	7.484	7.494	7.500	7.510	7.474	7.485	7.520	7.488
	Mixed Venous pH	7.390	7.410	7.427	7.430	7.427	7.428	7.450	7.451	7.409	7.434	7.434	7.435	7.434	7.447	7.465	7.466
7	Arterial pH	7.431	7.464	7.484	7.491	7.492	7.467	7.464	7.455	7.437	7.472	7.469	7.489	7.479	7.450	7.450	--
	Mixed Venous pH	7.381	7.452	7.443	7.445	7.455	7.429	7.424	7.424	7.370	7.392	7.393	7.434	7.444	7.431	7.436	--
8	Arterial pH	7.414	7.413	7.413	7.402	7.444	7.433	7.430	7.425	7.444	7.463	7.466	7.445	7.460	7.436	7.433	7.438
	Mixed Venous pH	7.354	7.369	7.363	7.366	7.404	7.406	7.384	7.390	7.366	7.389	7.401	7.402	7.443	7.409	7.401	7.400
9	Arterial pH	7.466	7.492	7.495	7.500	7.433	7.431	7.445	7.459	7.465	7.535	7.562	7.548	7.430	7.434	7.476	7.437
	Mixed Venous pH	7.409	7.434	7.445	7.440	7.402	7.425	7.413	7.430	7.383	7.455	7.492	7.479	7.433	7.403	7.409	7.399
10	Arterial pH	7.454	7.469	7.499	7.502	7.439	7.462	7.477	7.479	7.425	7.496	7.488	7.462	7.587	7.454	7.465	7.487
	Mixed Venous pH	7.392	7.406	7.454	7.445	7.448	7.448	7.440	7.446	7.377	7.420	7.406	7.377	7.569	7.433	7.440	7.455
$\bar{X}$	Arterial pH	7.440	7.453	7.463	7.470	7.447	7.453	7.461	7.461	7.441	7.481	7.488	7.491	7.462	7.446	7.461	7.464
	Mixed Venous pH	7.384	7.403	7.414	7.421	7.433	7.432	7.427	7.431	7.373	7.411	7.421	7.426	7.442	7.420	7.428	7.416
SE	Arterial pH	.007	.008	.009	.011	.009	.005	.008	.008	.007	.009	.011	.016	.017	.005	.012	.010
	Mixed Venous pH	.007	.009	.010	.009	.016	.009	.008	.008	.007	.009	.011	.012	.017	.005	.009	.010

APPENDIX TABLE 4

EXPERIMENT I. UNCORRECTED ARTERIAL AND MIXED VENOUS PLASMA $[HCO_3^-]$ (mM)

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

TIME (MIN)

Bird No.	$[HCO_3^-]$	Control				Ex I				Rest				Ex II				Rest				Ex II				Rest			
		0	30	45	55	2	10	15	20	10	10	60	90	2	10	15	20	10	30	60	90	2	10	15	20	10	30	60	90
1	A	20.7	19.2	19.8	19.2	17.9	17.5	17.2	17.2	18.0	18.6	19.8	19.3	18.8	16.5	15.9	13.4	18.6	17.8	19.1	19.1	16.7	15.3	14.6	16.4	16.2	18.8	22.2	22.7
	V	18.9	20.1	19.9	20.3	19.5	19.1	18.8	18.9	19.7	19.8	19.2	19.9	19.9	18.9	17.1	15.9	18.2	21.5	19.0	19.3	18.1	17.2	16.0	15.5	17.4	19.5	23.4	21.0
2	A	21.2	20.2	19.6	19.6	18.1	16.8	16.9	17.0	19.4	19.5	21.5	19.2	18.3	18.5	17.7	17.7	19.2	20.2	19.8	19.0	17.5	17.1	16.4	14.8	19.4	20.2	25.6	24.0
	V	20.5	20.9	18.9	21.5	19.9	20.3	19.2	19.6	18.9	21.5	20.7	18.6	20.4	19.4	19.6	19.1	20.5	18.3	21.1	20.7	19.8	18.9	17.6	17.2	19.6	21.5	23.1	25.0
3	A	20.4	21.0	16.9	20.8	17.4	16.5	----	15.8	17.0	18.2	20.2	18.7	16.6	14.7	13.7	13.3	----	----	20.7	20.4	11.5	11.5	11.0	----	----	----	----	----
	V	29.2	19.5	22.4	21.0	20.7	16.5	18.3	16.9	18.6	26.5	21.1	19.8	----	16.1	16.7	15.4	17.6	----	18.2	23.3	15.3	15.1	15.1	----	----	----	----	----
4	A	24.0	20.5	22.9	19.4	20.2	18.0	18.9	18.4	16.9	20.1	20.0	21.0	19.3	17.7	17.7	18.3	19.9	20.2	19.8	21.0	17.1	13.6	13.2	13.2	16.2	19.2	19.0	19.5
	V	21.7	21.4	21.4	21.9	20.2	20.5	19.8	20.1	19.5	19.3	20.4	21.0	20.4	19.8	18.3	18.6	26.4	20.5	18.8	22.1	19.0	17.3	15.5	15.9	17.8	19.7	18.5	27.9
5	A	21.2	20.0	19.9	20.2	15.2	15.0	14.5	14.8	17.0	18.6	17.9	18.8	16.3	14.6	14.1	13.6	15.4	17.7	19.7	20.3	15.1	13.4	12.1	11.8	14.3	18.6	18.4	18.1
	V	23.6	20.0	21.6	20.4	19.0	16.9	16.7	16.8	18.4	19.0	20.1	19.5	19.0	16.6	16.4	15.9	16.8	19.1	21.1	21.3	18.5	14.8	14.9	13.7	16.1	18.2	19.5	19.2
6	A	21.3	22.3	20.7	20.4	19.0	19.0	17.4	17.4	18.3	22.5	21.1	21.6	16.8	17.5	16.6	15.9	18.2	20.3	20.0	20.6	17.7	15.7	14.9	14.7	17.5	19.3	18.1	20.4
	V	23.0	20.6	20.6	19.5	20.2	19.2	19.5	18.4	19.6	19.5	22.5	20.7	20.3	17.9	18.1	16.7	19.3	19.9	21.7	21.2	20.2	18.0	17.4	16.3	18.1	19.1	20.4	20.4
7	A	21.1	21.1	20.3	20.4	17.5	17.8	17.0	17.9	17.7	19.3	18.9	18.6	16.0	17.6	16.6	16.8	18.2	20.3	19.6	19.5	16.0	14.3	13.3	13.2	15.4	17.8	19.3	----
	V	20.6	20.5	20.4	20.2	18.8	17.4	17.4	17.7	17.6	19.8	18.6	18.4	18.0	19.3	18.8	17.8	18.8	18.6	20.5	19.1	17.3	14.4	14.2	14.5	15.4	17.7	20.6	----
8	A	17.9	19.2	19.7	19.2	17.9	15.6	17.4	16.0	17.0	17.3	17.9	17.7	17.2	15.8	16.3	15.6	18.4	18.8	19.8	19.0	16.8	15.3	16.0	15.6	17.9	18.1	19.4	17.7
	V	19.6	19.6	19.7	20.1	16.9	17.3	15.8	17.4	17.2	18.5	17.0	18.3	16.7	17.7	16.1	16.2	18.1	20.4	19.1	19.5	18.0	16.5	16.7	16.5	17.4	20.5	17.5	18.5
9	A	20.6	19.9	20.2	19.1	16.1	15.7	15.5	14.9	18.0	18.2	17.0	18.5	16.0	13.8	13.4	13.0	16.2	18.3	17.6	18.4	15.9	13.1	13.5	13.5	17.2	18.5	18.5	18.0
	V	21.1	22.3	19.3	19.7	16.4	15.9	16.2	16.8	18.5	18.2	19.4	20.3	17.0	16.7	14.2	14.9	15.3	19.3	17.5	20.1	18.5	16.2	14.8	15.7	17.0	19.2	18.5	18.1
10	A	21.5	20.0	20.4	19.3	20.0	18.7	17.8	17.2	19.8	20.7	20.4	21.2	19.0	16.1	15.4	14.6	17.6	19.4	20.1	20.3	18.3	11.6	12.8	11.0	12.1	17.7	20.0	19.7
	V	20.0	20.8	19.6	20.3	19.8	20.0	19.0	18.4	18.9	21.8	20.5	22.1	18.5	17.7	15.8	16.3	16.6	20.8	19.4	20.7	19.6	15.9	14.5	13.7	12.4	18.2	20.2	20.5
$\bar{X}$	A	21.0	20.3	20.0	19.8	17.9	17.1	16.8	16.7	17.9	19.3	19.5	19.5	17.4	16.3	15.7	15.2	17.8	19.1	19.6	19.8	16.3	14.3	13.8	13.7	16.1	18.6	20.0	19.9
	V	21.8	20.6	20.4	20.5	19.1	18.3	18.1	18.1	18.7	20.4	19.9	19.9	18.9	18.0	17.2	16.7	18.8	19.9	19.6	20.7	18.4	16.4	15.7	15.5	16.8	19.3	20.2	20.9
SE	A	.47	.30	.46	20	.39	.39	.41	.39	.39	39	.39	.39	.39	.39	.39	.39	.41	.41	.39	.39	.39	.39	.39	.41	.41	.41	.41	.44
	V	.94	.27	.35	.24	.46	.46	.46	.46	.46	.46	.46	.46	.48	.46	.46	.46	.46	.48	.46	.46	.46	.46	.46	.48	.48	.48	.48	.51

APPENDIX TABLE 5

EXPERIMENT II. HEART RATE (BEATS·MIN^{-1}) AND MEAN ARTERIAL BLOOD PRESSURE (mm Hg) AT REST AND DURING EXERCISE WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

		Time (Min)																			
		Control				Ex I				Rest				Ex II				Rest			
		0	30	45	55	2	10	15	20	10	30	60	90	2	10	15	20	10	30	60	90
1	Heart Rate	235	248	251	260	434	418	361	378	290	295	263	297	465	457	454	431	284	---	288	274
	Mean Blood Pressure	118	108	115	103	164	164	157	160	152	155	145	128	164	164	163	160	136	---	121	150
2	Heart Rate	214	201	212	208	358	306	311	301	199	232	229	217	338	346	341	250	190	192	211	---
	Mean Blood Pressure	113	127	111	103	156	151	151	147	109	114	103	110	160	158	152	128	110	112	111	---
3	Heart Rate	286	264	271	286	517	506	511	448	252	248	259	236	516	546	529	499	298	322	230	241
	Mean Blood Pressure	101	113	107	105	160	145	151	146	106	105	109	111	154	155	150	155	142	132	106	108
4	Heart Rate	144	159	148	166	437	438	430	390	161	169	165	195	428	448	463	458	186	161	130	175
	Mean Blood Pressure	114	94	99	107	145	130	131	135	86	85	95	114	145	155	147	143	106	94	107	112
5	Heart Rate	274	292	---	244	473	474	461	468	365	294	282	296	487	492	488	498	353	368	334	359
	Mean Blood Pressure	82	73	---	63	132	130	108	117	90	70	73	73	143	129	125	139	87	86	90	108
6	Heart Rate	132	134	136	157	369	424	425	429	239	207	207	242	477	482	472	502	265	226	183	161
	Mean Blood Pressure	120	111	117	110	151	148	146	144	134	135	144	135	144	137	138	135	138	136	127	117
7	Heart Rate	276	270	260	324	469	445	468	469	354	339	354	322	510	481	459	500	349	356	315	325
	Mean Blood Pressure	162	135	132	143	157	128	143	157	157	145	130	150	152	140	142	153	122	142	130	133
8	Heart Rate	262	244	228	240	416	443	429	434	275	267	317	268	516	534	534	534	363	272	276	271
	Mean Blood Pressure	155	154	148	142	145	143	148	144	121	118	132	109	123	129	136	150	132	119	126	138
9	Heart Rate	268	275	305	297	478	398	370	378	317	299	321	287	497	458	436	468	329	332	321	302
	Mean Blood Pressure	88	92	89	100	141	125	123	126	115	99	110	103	133	128	128	128	126	110	103	109
10	Heart Rate	217	---	230	231	434	420	424	419	259	255	266	262	465	488	480	489	342	315	313	289
	Mean Blood Pressure	126	---	100	105	149	146	142	144	102	72	74	85	142	139	139	143	134	96	101	100
$\bar{X}$	Heart Rate	231	233	232	241	438	427	419	411	271	261	266	262	470	473	466	463	296	282	260	257
	Mean Blood Pressure	118	111	110	108	150	141	140	142	117	110	111	112	146	143	142	143	123	116	112	120
SE	Heart Rate	12.0	12.7	12.7	12.0	12.0	12.0	12.0	12.0	12.0	12.0	12.0	12.0	12.0	12.0	12.0	12.0	12.0	12.7	12.0	12.7
	Mean Blood Pressure	4.2	4.5	4.5	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.5	4.2	4.5

APPENDIX TABLE 6

EXPERIMENT 11. SYSTOLIC BLOOD PRESSURE (mm Hg) and DIASTOLIC BLOOD PRESSURE (mm Hg) AT REST AND DURING EXERCISE WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

Bird No.		Time (Min) Control 0	30	45	55	Ex I 2	10	15	20	Rest 10	30	60	90	Ex II 2	10	15	20	Rest 10	30	60	90
1	Systolic Pressure	142	133	153	130	185	193	190	187	175	185	185	165	202	202	203	187	181	---	184	199
	Diastolic Pressure	106	95	96	90	153	149	140	146	140	140	125	110	145	145	143	147	113	---	90	125
2	Systolic Pressure	142	155	134	139	183	178	180	175	142	146	127	130	175	175	173	143	135	127	140	---
	Diastolic Pressure	98	113	99	85	142	138	137	133	92	98	91	100	153	150	142	120	97	105	97	---
3	Systolic Pressure	142	154	152	140	194	185	187	184	157	155	158	162	196	199	200	215	193	182	175	173
	Diastolic Pressure	80	92	85	87	143	124	133	127	80	80	85	85	133	133	125	125	117	107	72	75
4	Systolic Pressure	147	134	138	144	174	160	164	175	135	133	138	147	181	183	184	180	151	149	170	172
	Diastolic Pressure	97	74	79	88	130	115	115	115	61	61	73	98	127	141	129	125	83	67	75	82
5	Systolic Pressure	110	103	---	104	167	170	147	150	116	109	115	128	179	169	168	198	147	141	155	165
	Diastolic Pressure	68	58	---	43	115	110	88	101	77	50	52	46	125	109	104	110	57	59	58	80
6	Systolic Pressure	165	164	176	165	184	183	183	193	175	186	190	180	183	175	176	185	190	189	178	175
	Diastolic Pressure	98	84	88	83	134	131	128	120	113	110	121	113	125	118	119	110	112	110	102	88
7	Systolic Pressure	184	168	165	178	190	166	180	200	190	180	159	180	183	169	177	190	157	173	160	170
	Diastolic Pressure	150	118	115	125	140	109	125	135	140	128	115	135	137	125	125	135	102	126	115	115
8	Systolic Pressure	175	175	175	173	165	170	173	170	163	157	175	158	163	172	178	200	175	183	185	190
	Diastolic Pressure	145	144	135	126	135	130	135	131	100	99	110	85	103	108	115	125	110	88	97	113
9	Systolic Pressure	136	140	137	140	184	170	170	182	159	145	160	153	180	180	180	195	173	155	153	163
	Diastolic Pressure	65	68	65	80	120	103	100	99	93	76	85	78	110	103	103	95	103	88	78	83
10	Systolic Pressure	157	---	135	145	176	177	174	177	148	128	123	140	181	178	180	190	175	148	163	164
	Diastolic Pressure	110	---	83	85	135	130	126	128	80	45	50	58	123	120	118	120	113	70	70	68
$\bar{X}$	Systolic Pressure	149	147	149	146	180	175	175	179	156	152	153	154	182	180	182	188	168	162	166	173
	Diastolic Pressure	102	93	91	89	135	124	123	123	98	89	91	91	128	125	122	121	101	93	85	93
SE	Systolic Pressure	4.20	4.44	4.44	4.20	4.20	4.20	4.20	4.20	4.20	4.20	4.20	4.20	4.20	4.20	4.20	4.20	4.44	4.20	4.20	4.44
	Diastolic Pressure	4.67	4.93	4.93	4.67	4.67	4.67	4.67	4.67	4.67	4.67	4.67	4.67	4.67	4.67	4.67	4.67	4.67	4.93	4.67	4.93

APPENDIX TABLE 7

EXPERIMENT II. RESPIRATORY TIDAL VOLUME (ml) BTPS

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

Bird No.	Time (Min)																			
	Control				Ex I				Rest				Ex II				Rest			
	0	30	45	55	2	10	15	20	10	30	60	90	2	10	15	20	10	30	60	90
1	102.3	109.3	104.4	100.9	72.2	53.2	24.6	24.6	45.3	75.8	89.3	71.1	94.1	22.5	22.0	23.6	16.0	----	----	18.2
2	48.2	182.2	168.4	110.4	115.1	40.2	33.0	29.3	24.9	277.6	259.0	243.7	75.1	32.1	23.7	22.5	15.8	92.0	116.9	104.3
3	49.2	61.8	61.8	65.9	38.9	29.9	28.3	23.0	14.3	22.9	58.0	61.4	38.5	24.8	21.2	21.4	18.9	12.5	13.4	34.9
4	73.9	84.3	107.4	83.2	57.2	35.0	28.1	24.8	36.3	81.7	98.7	121.1	90.0	51.3	43.9	42.2	32.3	174.2	150.4	150.9
5	81.7	98.0	----	108.2	48.5	26.1	25.8	22.8	18.4	23.8	29.8	26.1	47.4	33.5	30.8	33.6	16.0	18.8	23.3	26.8
6	119.9	131.8	129.3	187.0	83.6	43.2	33.1	32.6	19.1	112.4	96.2	93.5	89.0	39.6	37.7	39.7	32.3	146.7	116.9	162.8
7	91.4	75.9	60.5	44.0	48.8	25.5	25.7	23.4	24.6	58.2	53.2	66.0	44.4	33.8	30.8	29.8	37.9	48.8	56.4	64.3
8	77.2	75.6	71.2	64.3	51.9	42.0	32.0	28.5	51.5	59.2	62.2	62.6	73.3	54.3	39.8	34.6	50.5	84.3	91.5	107.6
9	85.3	67.5	58.5	45.4	43.3	24.1	12.3	34.3	48.1	67.8	62.0	73.3	42.9	29.7	23.8	20.3	31.0	77.6	62.7	67.2
10	59.1	----	93.8	85.7	53.4	20.2	18.7	18.8	32.8	66.4	87.0	99.6	44.7	22.9	23.5	24.6	13.6	126.9	77.4	126.2
$\bar{X}$	78.8	98.2	92.6	89.5	61.3	33.9	26.2	26.2	31.5	84.6	89.5	91.8	63.9	34.4	29.7	29.2	26.4	86.8	78.7	86.3
SE	9.79	10.35	10.35	9.79	9.79	9.79	9.79	9.79	9.79	9.79	9.79	9.79	9.79	9.79	9.79	9.79	9.79	10.35	10.35	9.79

APPENDIX TABLE 8

EXPERIMENT II. RESPIRATORY FREQUENCY (BREATHS·MIN^{-1})

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

Bird No.	Time (Min)																			
	Control				Ex I				Rest				Ex II				Rest			
	0	30	45	55	2	10	15	20	10	30	60	90	2	10	15	20	10	30	60	90
1	5.3	4.3	4.7	4.7	17.9	38.6	94.8	96.6	8.3	8.0	6.6	8.5	16.0	139.0	155.7	164.3	74.9	----	6.3	12.9
2	17.7	5.3	8.8	9.2	21.3	94.1	126.3	145.9	106.8	5.0	4.3	4.3	32.2	93.1	139.7	149.3	145.3	9.4	9.4	7.1
3	34.6	16.6	20.3	19.3	103.5	157.8	172.5	208.5	298.6	99.5	22.0	15.6	109.1	168.1	190.4	168.2	250.1	232.7	151.1	29.8
4	13.3	12.4	9.7	14.5	62.7	115.4	149.9	163.7	63.0	13.8	11.9	10.7	58.3	109.3	133.5	149.7	80.9	6.5	7.8	9.1
5	14.9	14.1	----	13.6	99.2	200.8	203.4	208.4	188.9	116.3	82.4	113.8	120.6	164.8	180.9	169.6	225.0	180.7	129.3	94.0
6	13.0	10.4	9.5	7.0	45.0	143.7	181.6	191.1	226.3	11.3	11.5	12.3	51.6	161.0	184.6	208.1	94.9	9.8	14.8	6.5
7	10.3	16.5	16.0	31.6	57.3	146.3	153.7	162.5	82.6	34.5	24.2	26.6	88.4	126.6	152.1	155.8	42.5	33.0	21.7	22.2
8	11.0	10.0	10.6	11.2	43.5	76.6	118.0	125.9	15.6	16.4	15.3	16.0	54.6	71.1	113.4	131.5	24.8	10.8	11.1	9.6
9	11.6	18.5	17.6	26.9	68.2	122.7	144.6	82.4	25.4	16.4	16.4	14.1	71.9	119.0	164.7	196.9	57.6	13.5	16.9	16.0
10	17.2	----	11.1	13.2	59.4	178.8	213.6	209.9	53.2	18.7	13.6	11.1	103.5	207.5	212.3	214.4	255.2	8.4	15.2	7.9
$\bar{X}$	14.9	13.8	18.0	15.1	57.8	127.5	155.8	159.5	106.9	34.0	20.8	23.3	70.6	135.9	162.7	170.8	125.1	52.6	38.4	21.5
SE	11.5	12.1	12.1	11.5	11.5	11.5	11.5	11.5	11.5	11.5	11.5	11.5	11.5	11.5	11.5	11.5	11.5	12.1	11.5	11.5

APPENDIX TABLE 9

EXPERIMENT II. RESPIRATORY MINUTE VOLUME ($l \cdot min^{-1}$) BTPS

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

	Time (min)																			
	Control				Ex I				Rest				Ex II				Rest			
Bird No.	0	30	45	55	2	10	15	20	10	30	60	90	2	10	15	20	10	30	60	90
1	.54	.47	.49	.47	1.29	2.05	2.33	2.38	.38	.61	.59	.60	1.51	3.13	3.43	3.88	1.20	----	----	.23
2	.85	.97	1.48	1.02	2.45	3.78	4.17	4.27	2.66	1.39	1.11	1.05	2.42	2.99	3.31	3.36	2.30	.86	1.10	.74
3	1.70	1.03	1.25	1.27	4.03	4.72	4.88	4.80	4.27	2.28	1.28	.96	4.20	4.17	4.02	3.60	4.73	2.91	2.02	1.04
4	.98	1.05	1.04	1.21	3.59	4.04	4.21	4.06	2.29	1.13	1.17	1.30	5.25	5.61	5.86	6.32	2.61	1.13	1.17	1.37
5	1.22	1.38	----	1.47	4.81	5.24	5.25	4.75	3.48	2.77	2.46	2.97	5.72	5.52	5.57	5.70	3.60	3.40	3.01	2.52
6	1.56	1.37	1.23	1.31	3.72	6.21	6.01	6.23	4.32	1.27	1.11	1.15	4.59	6.38	6.96	8.26	3.07	1.44	1.73	1.06
7	.94	1.25	.97	1.39	2.80	3.73	3.95	3.80	2.03	2.01	1.29	1.76	3.93	4.28	4.68	4.64	1.61	1.61	1.22	1.43
8	.85	.76	.75	.72	2.26	3.22	3.78	3.59	.80	.97	.95	1.00	4.00	3.86	4.51	4.55	1.25	.91	1.02	1.03
9	.99	1.25	1.03	1.22	2.95	2.96	1.78	2.83	1.22	1.11	1.02	1.03	3.08	3.53	3.92	4.00	1.79	1.05	1.06	1.08
10	1.02	----	1.04	1.13	3.17	3.61	3.99	3.95	1.75	1.24	1.18	1.11	4.63	4.75	5.00	5.27	3.47	1.07	1.18	1.00
$\bar{X}$	1.07	1.06	1.16	1.03	3.11	3.96	4.04	4.07	2.32	1.48	1.21	1.30	3.93	4.42	4.73	4.96	2.56	1.60	1.50	1.15
SE	.21	.22	.22	.10	.21	.21	.21	.21	.21	.21	.21	.21	.21	.21	.21	.21	.21	.31	.22	.21

APPENDIX TABLE 10

EXPERIMENT II. ARTERIAL AND MIXED VENOUS PCO_2 BLOOD GAS TENSIONS (torr)

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

Bird No.		Control 0	Control 30	Control 45	Control 55	Ex I 2	Ex I 10	Ex I 15	Ex I 20	Rest 10	Rest 30	Rest 60	Rest 90	Ex II 2	Ex II 10	Ex II 15	Ex II 20	Rest 10	Rest 30	Rest 60	Rest 90
		Time (Min)																			
1	Arterial PCO_2	26.1	24.4	29.7	27.1	28.8	21.8	23.5	20.5	23.8	27.5	34.6	26.8	29.1	21.0	18.5	16.7	22.5	----	24.7	26.5
	Mixed Venous PCO_2	27.5	32.7	28.3	33.3	35.4	30.5	27.2	26.9	30.3	35.1	34.5	36.9	34.9	27.7	23.2	22.3	26.1	----	28.7	30.2
2	Arterial PCO_2	22.2	26.4	26.1	24.6	26.4	25.0	22.2	24.1	22.7	24.7	27.2	29.6	28.3	25.4	26.1	25.4	25.2	20.0	24.7	27.7
	Mixed Venous PCO_2	25.6	33.0	28.5	31.2	33.1	35.4	31.6	31.4	27.7	30.2	28.9	32.8	35.2	36.3	32.9	32.2	27.7	28.2	27.7	31.1
3	Arterial PCO_2	24.6	25.1	20.1	24.9	25.4	24.1	21.5	22.0	22.7	26.2	23.0	25.0	23.0	22.0	20.5	17.4	15.7	19.2	23.5	20.6
	Mixed Venous PCO_2	31.9	28.6	25.3	29.1	34.1	30.2	29.8	27.1	27.7	29.7	29.4	28.9	33.2	29.6	28.3	25.2	21.6	23.4	29.3	25.4
4	Arterial PCO_2	25.0	18.9	22.5	16.4	22.6	21.2	23.2	20.3	18.0	17.6	19.4	23.6	21.7	17.7	19.5	16.8	18.4	19.8	19.4	19.5
	Mixed Venous PCO_2	27.4	27.1	24.4	26.6	29.9	29.5	26.5	26.7	22.4	25.5	23.5	29.1	28.3	27.4	26.0	25.3	25.7	26.4	24.5	25.5
5	Arterial PCO_2	25.7	22.5	----	21.2	22.5	19.4	16.5	18.4	21.8	22.4	20.6	23.1	20.3	21.0	20.2	20.4	20.5	22.5	24.6	25.3
	Mixed Venous PCO_2	29.9	29.5	----	27.4	28.8	27.7	25.0	24.9	25.3	29.9	26.2	27.8	28.3	27.9	25.4	26.1	22.5	26.9	27.7	29.8
6	Arterial PCO_2	15.8	16.9	20.7	23.4	24.6	24.3	22.0	21.3	23.8	18.5	24.7	21.8	24.6	22.4	19.7	16.0	21.9	18.5	18.4	23.3
	Mixed Venous PCO_2	18.7	22.9	22.8	27.0	29.9	30.3	27.9	28.6	26.2	25.6	27.6	27.6	28.5	29.1	25.1	20.8	25.3	24.3	21.8	25.2
7	Arterial PCO_2	24.3	22.9	23.3	25.1	22.3	20.9	19.6	19.7	19.8	20.5	24.5	19.3	19.2	19.5	19.5	17.4	23.9	----	23.9	22.0
	Mixed Venous PCO_2	32.6	25.3	27.2	29.0	26.1	26.3	26.2	26.3	26.1	22.9	26.7	24.1	30.5	27.6	27.3	23.0	27.2	33.6	28.2	28.4
8	Arterial PCO_2	29.3	25.4	29.1	27.7	25.4	21.2	21.3	19.8	24.8	21.7	24.9	17.6	20.8	18.1	17.6	14.9	22.0	22.2	20.4	18.5
	Mixed Venous PCO_2	30.9	32.1	31.3	33.6	31.6	31.1	26.3	26.2	27.5	29.0	26.6	23.4	28.9	28.5	25.1	23.6	24.7	25.1	22.2	23.8
9	Arterial PCO_2	27.7	28.4	24.5	28.4	25.2	23.8	23.0	21.3	25.4	23.9	27.8	25.6	22.9	24.7	22.0	23.0	26.2	25.0	24.7	26.6
	Mixed Venous PCO_2	33.8	33.3	33.5	29.8	32.1	29.0	28.5	27.6	29.4	28.2	32.0	27.6	32.8	287.7	29.7	27.7	30.4	28.4	29.6	29.1
10	Arterial PCO_2	30.2	----	24.4	25.5	24.3	26.5	25.3	22.0	25.1	21.9	24.4	24.9	26.0	21.3	20.5	19.2	20.8	22.7	25.0	26.6
	Mixed Venous PCO_2	32.5	----	30.0	29.1	32.9	29.8	31.1	30.1	30.3	26.3	29.5	28.5	34.4	27.2	28.7	24.8	25.9	28.6	28.1	29.0
$\bar{X}$	Arterial PCO_2	25.1	23.6	24.4	24.4	24.7	22.8	21.8	20.9	22.8	22.5	25.1	23.7	23.6	21.3	20.4	18.7	21.7	21.3	22.9	23.7
	Mixed Venous PCO_2	29.1	29.5	27.8	29.6	31.4	30.0	28.0	27.6	27.3	28.2	28.5	28.7	31.5	29.0	27.2	25.1	25.7	27.4	26.8	27.7
SE	Arterial PCO_2	.78	.82	.82	.78	.78	.78	.78	.78	.78	.78	.78	.78	.78	.78	.78	.78	.78	.78	.78	.78
	Mixed Venous PCO_2	.79	.83	.83	.79	.79	.79	.79	.79	.79	.79	.79	.79	.79	.79	.79	.79	.79	.83	.79	.79

APPENDIX TABLE 11

EXPERIMENT II. ARTERIAL AND MIXED VENOUS PO_2 BLOOD GAS TENSIONS (torr)
AT REST AND DURING EXERCISE
WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

		Time (Min)																			
		Control				Ex I					Rest			Ex II				Rest			
		0	30	45	55	2	10	15	20	10	30	60	90	2	10	15	20	10	30	60	90
1	Arterial PO_2	92.6	90.3	85.1	88.7	98.5	100.6	102.7	102.2	110.5	96.4	102.5	99.8	109.4	110.1	115.8	112.3	115.3	----	101.2	100.4
	Mixed Venous PO_2	52.0	56.1	50.3	58.2	42.3	47.2	45.2	44.2	58.0	60.8	59.8	64.7	46.2	49.0	44.7	43.0	-----	----	59.8	48.5
2	Arterial PO_2	113.3	93.5	96.4	101.7	98.7	96.8	103.2	95.7	107.9	89.9	112.2	86.8	106.3	99.1	102.3	102.0	109.7	111.9	113.9	96.0
	Mixed Venous PO_2	57.6	61.2	54.5	57.5	42.7	48.1	47.4	44.6	56.0	59.6	60.2	62.8	45.5	47.8	46.2	44.6	56.1	63.0	59.6	62.8
3	Arterial PO_2	104.4	114.0	103.1	104.2	97.1	103.0	109.9	98.5	98.9	108.0	105.2	112.2	107.2	116.0	111.4	115.0	119.2	124.5	108.1	120.1
	Mixed Venous PO_2	62.1	56.7	55.8	51.7	46.9	45.8	44.8	44.9	55.2	56.3	62.2	60.0	54.1	53.8	54.3	53.9	63.1	62.5	67.1	56.1
4	Arterial PO_2	98.4	108.3	86.8	92.6	104.1	107.6	105.8	104.7	116.2	109.7	75.9	95.8	105.4	104.2	107.7	109.5	113.3	109.4	111.4	86.6
	Mixed Venous PO_2	51.7	56.2	49.8	50.4	42.2	47.5	47.5	47.2	55.4	56.9	47.0	53.8	41.0	44.4	43.9	46.4	56.0	59.3	54.4	53.7
5	Arterial PO_2	86.9	79.1	-----	88.0	86.9	85.4	90.2	84.8	98.3	95.1	96.0	90.1	103.4	101.4	106.9	102.9	114.3	105.3	112.0	98.7
	Mixed Venous PO_2	43.1	45.9	-----	41.6	36.3	38.7	37.2	36.8	52.2	53.2	46.5	50.3	42.9	48.0	50.8	47.7	59.7	64.2	60.3	62.2
6	Arterial PO_2	103.4	98.0	81.3	80.7	95.3	98.5	101.2	97.2	97.0	98.5	99.4	96.6	103.3	100.1	100.5	98.7	101.2	94.4	104.1	89.5
	Mixed Venous PO_2	48.5	55.4	52.1	58.5	50.3	56.3	53.0	53.5	60.0	62.6	62.2	66.1	53.4	55.6	50.6	48.5	62.2	60.9	56.2	55.5
7	Arterial PO_2	105.5	119.0	105.7	109.9	108.4	113.2	116.0	115.6	111.2	107.0	----	133.2	124.4	136.3	127.5	133.0	121.5	122.0	136.4	130.3
	Mixed Venous PO_2	60.9	64.2	63.1	66.2	52.9	53.2	54.6	53.7	54.3	52.9	69.6	68.8	61.7	62.2	61.7	61.2	73.7	70.5	80.2	77.9
8	Arterial PO_2	107.6	105.7	108.9	105.6	113.6	117.7	119.8	117.4	110.9	120.0	103.2	119.4	119.1	121.2	128.5	134.1	122.5	118.9	127.9	126.6
	Mixed Venous PO_2	61.8	66.6	63.5	68.3	52.4	57.8	56.5	54.1	64.6	70.9	58.8	70.5	54.2	55.2	62.0	60.5	70.0	78.1	69.7	72.0
9	Arterial PO_2	89.1	97.4	95.2	88.9	91.4	102.8	96.7	99.2	91.1	101.6	89.2	93.6	91.8	102.8	100.4	100.8	91.5	101.5	97.5	101.2
	Mixed Venous PO_2	49.0	50.2	53.9	49.0	45.0	48.2	46.8	45.4	56.4	52.7	56.8	51.2	45.9	47.5	49.1	48.3	59.8	55.1	60.9	55.9
10	Arterial PO_2	108.2	-----	88.4	113.1	104.2	112.8	109.7	111.7	107.0	118.2	101.8	110.1	108.8	118.6	115.6	119.5	112.5	112.4	105.5	108.5
	Mixed Venous PO_2	58.5	-----	57.7	58.0	52.4	54.6	55.8	54.1	62.4	56.1	60.0	58.7	53.8	53.2	53.9	54.0	63.3	61.8	63.6	59.5
$\bar{X}$	Arterial PO_2	100.9	101.1	93.5	97.3	99.8	103.8	105.5	102.7	104.9	104.4	100.0	103.8	107.9	111.0	111.7	112.8	112.1	110.8	111.8	105.8
	Mixed Venous PO_2	54.5	57.2	54.9	55.9	46.3	49.7	48.9	47.8	57.4	58.2	58.3	60.7	49.9	51.7	51.7	50.8	62.4	63.6	63.2	60.4
SE	Arterial PO_2	2.13	2.25	2.25	2.13	2.13	2.13	2.13	2.13	2.13	2.13	2.25	2.13	2.13	2.13	2.13	2.13	2.13	2.25	2.13	2.13
	Mixed Venous PO_2	1.26	1.33	1.33	1.26	1.26	1.26	1.26	1.26	1.26	1.26	1.26	1.26	1.26	1.26	1.26	1.26	1.33	1.33	1.26	1.26

APPENDIX TABLE 12

EXPERIMENT II. ARTERIAL AND MIXED VENOUS pH
AT REST AND DURING EXERCISE
WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

Bird No.		Control				Ex I				Rest				Ex II				Rest			
	Time (Min)	0	30	45	55	2	10	15	20	10	30	60	90	2	10	15	20	10	30	60	90
1	Arterial pH	7.50	7.50	7.48	7.49	7.48	7.53	7.52	7.53	7.48	7.48	7.43	7.52	7.49	7.56	7.59	7.61	7.51	----	7.52	7.53
	Mixed Venous pH	7.46	7.48	7.48	7.45	7.42	7.45	7.48	7.47	7.45	7.44	7.45	7.46	7.44	7.50	7.53	7.56	7.50	----	7.51	7.50
2	Arterial pH	7.41	7.48	7.47	7.50	7.47	7.48	7.48	7.49	7.48	7.51	7.52	7.45	7.47	7.47	7.49	7.49	7.49	7.55	7.54	7.48
	Mixed Venous pH	7.51	7.47	7.49	7.49	7.43	7.43	7.44	7.44	7.48	7.46	7.48	7.44	7.41	7.42	7.44	7.44	7.48	7.49	7.50	7.47
3	Arterial pH	7.46	7.50	7.51	7.47	7.46	7.48	7.49	7.51	7.49	7.45	7.48	7.49	7.50	7.51	7.52	7.54	7.53	7.50	7.49	7.55
	Mixed Venous pH	7.47	7.44	7.49	7.45	7.40	7.44	7.44	7.46	7.46	7.44	7.44	7.47	7.44	7.46	7.47	7.47	7.49	7.47	7.47	7.53
4	Arterial pH	7.46	7.51	7.51	7.53	7.48	7.50	7.49	7.50	7.51	7.53	7.54	7.49	7.50	7.53	7.51	7.50	7.47	7.46	7.46	7.49
	Mxied Venous pH	7.45	7.47	7.49	7.51	7.41	7.44	7.43	7.45	7.47	7.51	7.51	7.47	7.44	7.45	7.48	7.49	7.47	7.43	7.44	7.45
5	Arterial pH	7.50	7.53	----	7.53	7.51	7.52	7.52	7.53	7.48	7.50	7.52	7.50	7.49	7.49	7.50	7.49	7.49	7.48	7.48	7.48
	Mixed Venous pH	7.49	7.51	----	7.50	7.46	7.46	7.48	7.47	7.47	7.48	7.51	7.48	7.44	7.43	7.44	7.42	7.45	7.47	7.46	7.47
6	Arterial pH	7.64	7.60	7.54	7.49	7.46	7.45	7.46	7.48	7.48	7.54	7.49	7.49	7.45	7.48	7.49	7.53	7.50	7.56	7.59	7.52
	Mixed Venous pH	7.60	7.53	7.52	7.49	7.43	7.40	7.43	7.43	7.47	7.52	7.48	7.49	7.41	7.43	7.45	7.47	7.47	7.53	7.45	7.49
7	Arterial pH	7.46	7.51	7.52	7.57	7.49	7.40	7.42	7.48	7.54	7.49	7.53	7.52	7.46	7.46	7.47	7.47	7.42	7.43	7.45	7.49
	Mixed Venous pH	7.44	7.50	7.53	7.46	7.47	7.38	7.35	7.45	7.56	7.51	7.43	7.49	7.41	7.41	7.41	7.42	7.40	7.40	7.41	7.47
8	Arterial pH	7.43	7.45	7.44	7.43	7.46	7.47	7.50	7.49	7.45	7.50	7.45	7.53	7.50	7.49	7.49	----	----	----	----	----
	Mixed Venous pH	7.42	7.39	7.43	7.42	7.42	7.43	7.44	7.45	7.43	7.45	7.44	7.52	7.43	7.45	7.47	----	----	----	----	----
9	Arterial pH	7.51	7.50	7.51	7.48	7.50	7.50	7.51	7.52	7.49	7.52	7.48	7.51	7.51	7.49	7.50	7.50	7.48	7.49	7.48	7.46
	Mixed Venous pH	7.49	7.46	7.48	7.47	7.45	7.45	7.48	7.46	7.48	7.49	7.46	7.49	7.45	7.45	7.45	7.46	7.45	7.47	7.45	7.45
10	Arterial pH	7.50	----	7.56	7.50	7.53	7.52	7.52	7.52	7.41	7.56	7.52	7.54	7.50	7.53	7.53	7.55	7.53	7.49	7.49	7.51
	Mixed Venous pH	7.48	----	7.51	7.53	7.48	7.48	7.48	7.48	7.48	7.53	7.50	7.51	7.45	7.48	7.47	7.50	7.51	7.47	7.50	----
$\bar{X}$	Arterial pH	7.49	7.51	7.50	7.50	7.48	7.48	7.49	7.50	7.49	7.51	7.50	7.49	7.49	7.50	7.51	7.52	7.49	7.49	7.49	7.50
	Mixed Venous pH	7.48	7.47	7.49	7.48	7.44	7.43	7.44	7.46	7.47	7.48	7.47	7.48	7.43	7.44	7.46	7.47	7.47	7.46	7.47	7.48
SE	Arterial pH	.020	.014	0.12	.011	.011	.011	.011	.011	.011	.011	.011	.011	.011	.011	.011	.012	.012	.012	.012	.012
	Mixed Venous pH	.016	.014	.010	.010	.010	.010	.010	.010	.010	.010	.010	.010	.010	.010	.010	.011	.011	.011	.011	.011

APPENDIX TABLE 13

EXPERIMENT II. ARTERIAL AND MIXED VENOUS PLASMA $[HCO_3^-]$ (mM)

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

Bird No.		Control 0	Control 30	Control 45	Control 55	Ex I 2	Ex I 10	Ex I 15	Ex I 20	Rest 10	Rest 30	Rest 60	Rest 90	Ex II 2	Ex II 10	Ex II 15	Ex II 20	Rest 10	Rest 30	Rest 60	Rest 90
1	A	18.9	17.8	20.4	19.2	19.7	16.8	17.8	16.0	16.3	19.0	21.4	20.4	20.7	17.5	16.5	15.6	16.6	----	18.6	20.7
	V	18.1	22.7	19.4	21.6	21.5	19.7	18.8	18.3	19.7	22.2	22.2	24.3	22.2	20.3	18.1	18.5	18.9	----	21.3	22.1
2	A	13.1	18.2	17.8	17.8	18.0	17.3	15.4	17.0	15.9	18.2	20.8	18.9	19.1	17.3	18.4	18.0	18.0	16.1	19.8	19.1
	V	19.0	22.5	20.4	21.8	20.2	21.7	19.9	19.9	19.2	20.1	20.0	20.9	20.7	21.8	20.5	20.3	19.0	20.1	19.9	21.0
3	A	16.2	18.0	14.8	16.8	16.8	16.8	15.3	16.4	16.2	16.8	15.9	17.7	16.5	16.2	15.7	13.9	12.1	14.0	16.6	16.6
	V	21.8	18.0	17.8	18.8	19.7	19.0	19.0	18.0	18.1	18.9	18.7	19.7	20.8	19.4	19.0	17.2	15.1	15.8	19.6	19.5
4	A	16.4	14.1	16.8	12.7	15.8	15.4	16.4	14.7	13.3	13.8	15.5	16.7	15.8	13.6	14.4	12.1	12.5	13.0	12.8	13.9
	V	17.7	18.2	17.3	19.7	17.6	18.5	16.4	16.9	15.0	19.0	17.4	19.5	17.9	17.7	18.1	17.8	17.5	16.1	15.5	16.5
5	A	18.6	17.6	----	16.3	16.6	14.6	12.5	14.2	15.1	16.1	15.5	16.7	14.4	14.9	14.6	14.3	14.6	15.4	17.1	17.5
	V	21.1	22.0	----	19.7	18.8	18.2	17.1	16.8	16.9	20.9	19.2	19.2	17.7	17.2	15.9	15.8	14.6	18.4	18.5	20.3
6	A	15.8	15.4	16.5	16.6	16.2	15.6	14.6	14.6	16.4	14.7	17.4	15.5	15.9	15.4	13.9	12.5	15.7	15.5	16.2	17.6
	V	17.2	17.9	17.4	19.3	18.3	17.5	17.2	17.6	17.6	19.4	19.2	19.3	16.8	17.9	16.1	14.1	17.0	18.9	17.6	17.9
7	A	16.1	16.9	17.7	21.1	15.8	12.0	11.8	13.6	15.8	14.6	19.0	14.5	12.6	12.8	13.1	11.7	14.2	----	15.3	15.5
	V	20.8	18.2	21.3	19.2	17.7	14.5	13.4	16.8	21.9	17.0	16.4	17.0	17.9	16.1	16.1	13.9	15.6	19.2	16.8	19.0
8	A	17.9	16.4	18.3	17.2	16.9	14.2	15.4	14.1	16.1	15.6	16.0	13.8	15.0	12.8	12.5	----	----	----	----	----
	V	18.4	18.1	19.3	20.1	19.0	19.1	16.8	16.9	16.8	18.7	16.8	17.6	17.7	17.3	16.8	----	----	----	----	----
9	A	20.7	20.6	18.1	19.6	18.1	17.3	16.9	16.0	18.0	18.1	19.3	19.1	16.9	17.6	15.9	16.8	18.1	17.8	16.9	17.7
	V	23.8	22.0	23.1	20.3	20.7	18.6	19.6	18.4	20.2	19.9	21.2	19.7	21.1	18.6	19.0	18.4	19.8	19.3	19.1	18.6
10	A	22.1	----	20.1	18.3	19.0	20.0	19.3	16.5	18.8	18.4	18.6	19.6	18.8	16.4	16.0	15.5	16.1	16.1	17.0	19.9
	V	22.3	----	22.5	22.4	22.6	20.6	21.6	20.6	20.9	20.3	21.5	20.9	22.1	18.7	19.3	18.0	19.3	19.2	20.8	----
$\bar{X}$	A	17.6	17.2	17.8	17.6	17.3	16.0	15.5	15.3	16.2	16.5	17.9	17.3	16.6	15.5	15.1	14.5	15.3	15.4	16.7	17.6
	V	20.0	20.0	19.8	20.3	19.6	18.7	18.0	18.0	18.7	19.6	19.3	19.8	19.5	18.5	17.9	17.1	17.4	18.4	18.8	19.4
SE	A	0.83	0.62	0.58	0.72	0.43	0.43	0.43	0.43	0.43	0.43	0.43	0.43	0.43	0.43	0.43	0.45	0.45	0.51	0.45	0.45
	V	0.71	0.75	0.72	0.39	0.41	0.41	0.41	0.41	0.41	0.41	0.41	0.41	0.41	0.41	0.41	0.44	0.44	0.47	0.44	0.47

APPENDIX TABLE 14

EXPERIMENT II. BODY TEMPERATURE (DEGREES CENTIGRADE)

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

Bird No.	Time (Min) Control 0	30	45	55	Ex I 2	10	15	20	Rest 10	30	60	90	Ex II 2	10	15	20	Rest 10	30	60	90
1	41.1	41.2	41.5	41.8	41.8	42.0	42.3	42.4	42.1	42.1	42.1	42.1	42.2	42.8	42.9	43.0	42.5	---	42.1	42.1
2	40.5	40.5	40.5	41.3	41.0	41.5	41.8	41.9	41.8	41.3	41.5	41.5	41.9	42.2	42.5	42.5	42.2	42.0	41.8	41.8
3	41.3	41.8	41.8	41.8	42.0	42.3	42.8	43.0	42.8	42.3	42.4	42.3	42.8	43.5	44.0	44.2	44.1	43.9	43.0	42.8
4	40.1	40.5	40.6	40.6	41.1	41.6	42.0	42.0	41.9	41.5	41.1	41.1	41.5	41.9	42.1	42.6	42.0	41.5	41.2	41.1
5	40.1	40.0	----	40.5	41.1	41.7	41.8	42.0	42.1	42.0	41.2	41.2	42.2	43.0	43.3	43.5	43.1	43.0	42.8	42.3
6	41.0	41.0	41.1	41.2	41.5	41.9	42.0	42.2	41.6	41.1	41.5	41.6	42.0	42.4	42.1	42.0	----	----	----	----
7	42.1	42.5	42.3	42.7	43.0	43.1	43.1	43.2	43.0	43.0	43.1	43.2	43.5	44.0	44.0	44.0	43.1	43.0	42.8	43.0
8	42.3	42.3	42.2	42.8	42.8	42.9	42.9	42.9	42.0	42.0	42.2	42.8	43.1	43.5	43.9	43.9	43.0	42.8	42.5	42.9
9	40.6	41.0	41.0	40.6	41.0	41.5	41.8	41.5	40.8	40.6	41.0	40.8	41.1	42.0	42.5	42.8	42.1	41.5	41.5	41.3
10	41.4	----	41.2	41.3	42.0	42.5	42.8	42.9	42.3	42.0	42.1	42.1	43.0	43.3	43.8	44.0	43.2	42.5	42.3	42.2
$\bar{X}$	41.0	41.2	41.3	41.5	41.7	42.1	42.3	42.4	42.0	41.8	41.8	41.9	42.3	42.9	43.1	43.2	42.8	42.5	42.2	42.1
SE	.11	.12	.12	.11	.11	.11	.11	.11	.11	.11	.11	.11	.11	.11	.11	.11	.12	.12	.12	.12

APPENDIX TABLE 15

EXPERIMENT III. ARTERIAL PCO_2 BLOOD GAS TENSIONS (torr)

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

BIRD NO.	CONTROL				EX I				REST				EX II				REST			
	TIME (MIN.)																			
	0	30	45	55	2	10	15	20	10	30	60	90	2	10	15	20	10	30	60	90
1	27.1	29.2	29.5	27.9	25.4	28.7	28.9	28.5	27.6	28.1	28.9	28.5	24.3	26.3	26.3	25.6	27.9	30.7	30.1	30.9
2	28.9	30.9	31.6	31.4	25.2	20.9	22.0	24.4	25.3	29.5	30.9	29.3	21.6	20.4	20.0	20.1	26.4	27.5	27.7	31.3
3	31.7	30.4	30.8	32.0	27.8	25.9	28.6	26.9	29.9	31.7	30.6	30.7	30.5	29.2	28.8	27.9	29.8	30.5	30.8	29.6
4	30.6	30.9	28.1	31.3	25.4	25.7	24.6	24.3	27.4	30.5	29.3	29.1	25.1	22.7	24.3	25.9	27.7	30.7	30.9	31.6
5	27.0	29.1	25.5	23.9	19.5	23.6	22.2	--	25.4	22.9	28.8	25.2	21.0	19.2	21.5	20.8	23.2	26.3	25.7	26.1
$\bar{X}$	29.1	30.1	29.1	29.3	24.7	25.0	25.3	25.2	27.1	28.5	29.7	28.6	24.5	23.6	24.2	24.1	27.0	29.1	29.0	29.9
SE	.96	.81	1.09	1.39	.80	.80	.80	.90	.80	.80	.80	.80	.80	.80	.80	.80	.80	.80	.80	.80

APPENDIX TABLE 16

EXPERIMENT III. ARTERIAL PO_2 BLOOD GAS TENSIONS (torr)

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

	Time (min)																			
	Control				Ex I				Rest				Ex II				Rest			
Bird No.	0	30	45	55	2	10	15	20	10	30	60	90	2	10	15	20	10	30	60	90
1	97.3	92.6	96.0	96.7	99.2	103.7	-	100.9	99.8	97.5	95.9	100.8	111.2	114.3	110.4	109.5	104.4	103.2	97.9	94.9
2	100.3	95.8	88.4	99.9	98.7	112.3	109.5	105.9	96.2	100.9	98.5	97.6	111.0	110.5	111.2	110.3	101.3	104.9	101.1	100.9
3	103.8	107.0	105.1	98.4	111.3	108.6	106.2	105.4	106.0	103.9	105.6	107.0	103.9	108.3	105.9	108.3	109.0	104.9	103.9	112.4
4	100.6	95.8	101.1	97.9	99.6	103.9	102.7	103.9	97.0	96.9	102.6	100.1	117.8	110.4	106.3	103.9	97.7	113.0	112.6	101.1
5	99.4	103.9	104.0	105.2	111.1	112.9	111.9	-	112.4	108.6	109.9	108.7	112.3	114.3	109.4	114.3	114.1	115.9	113.6	114.9
$\bar{X}$	100.3	99.0	98.9	99.6	104.0	108.3	106.7	105.4	102.3	101.6	102.5	102.8	111.2	111.6	108.6	109.3	105.3	108.4	105.8	104.8
SE	1.06	27.3	3.07	1.49	1.79	1.79	2.02	1.79	1.79	1.79	1.79	1.79	1.79	1.79	1.79	1.79	1.79	1.79	1.79	1.79

APPENDIX TABLE 17

EXPERIMENT III. ARTERIAL pH

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

BIRD NO.	CONTROL				EX I				REST				EX II				REST			
	TIME (MIN.)																			
	0	30	45	55	2	10	15	20	10	30	60	90	2	10	15	20	10	30	60	90
1	7.52	7.50	7.48	7.48	7.50	7.46	7.47	7.46	7.47	7.48	7.49	7.51	7.47	7.47	7.45	7.48	7.46	7.48	7.49	7.49
2	7.48	7.47	7.45	7.46	7.50	7.51	7.52	7.51	7.48	7.46	7.46	7.47	7.48	7.52	7.53	7.55	7.47	7.46	7.47	7.47
3	7.46	7.48	7.49	7.47	7.45	7.47	7.46	7.49	7.48	7.48	7.48	7.49	7.49	7.49	7.49	7.49	7.49	7.49	7.48	7.48
4	7.47	7.47	7.51	7.46	7.49	7.51	7.50	7.50	7.46	7.47	7.47	7.47	7.47	7.52	7.51	7.50	7.47	7.41	7.41	7.44
5	7.47	7.51	7.47	7.48	7.51	7.50	7.49	--	7.46	7.46	7.44	7.45	7.46	7.48	7.48	7.48	7.45	7.45	7.45	7.45
$\bar{X}$	7.48	7.49	7.48	7.47	7.49	7.49	7.49	7.49	7.47	7.47	7.47	7.48	7.48	7.49	7.49	7.50	7.47	7.46	7.46	7.47
SE.	.010	.008	.010	.004	.011	.011	.011	.013	.011	.011	.011	.011	.011	.011	.011	.011	.011	.011	.011	.011

APPENDIX TABLE 18

EXPERIMENT III. CLAVICULAR AIR SAC PCO_2 GAS TENSIONS (torr) AT REST AND DURING EXERCISE WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

BIRD NO.	CONTROL				EX I				REST		TIME (MIN.)		EX II				REST			
	0	30	45	55	2	10	15	20	10	30	60	90	2	10	15	20	10	30	60	90
1	34.7	36.9	35.9	38.5	32.9	31.9	34.5	33.4	37.1	35.3	37.6	37.5	29.4	29.7	28.0	--	34.5	38.5	37.8	37.3
2	38.0	40.1	39.5	41.5	31.2	25.0	27.3	27.8	32.3	37.6	37.6	37.8	26.7	24.2	24.3	23.8	31.8	34.8	35.9	35.3
3	37.9	37.2	37.5	38.8	32.7	31.5	32.8	31.5	34.4	37.0	37.7	35.4	35.0	31.7	30.2	31.5	33.4	32.9	33.9	33.9
4	39.3	38.5	39.0	40.1	34.5	30.6	29.5	31.0	33.9	37.1	37.3	36.8	30.3	28.4	28.5	29.0	33.3	35.0	35.4	35.2
5	34.5	35.3	33.5	33.3	27.9	26.1	27.3	25.8	30.3	31.2	33.6	31.1	25.7	22.3	24.4	24.8	30.4	33.2	31.7	32.0
$\bar{X}$	36.9	37.6	37.1	38.4	31.8	29.0	30.3	29.9	33.6	35.6	36.8	35.7	29.4	27.3	27.1	27.6	32.7	34.9	34.9	34.7
SE	.96	.81	1.09	1.39	.83	.83	.83	.83	.83	.83	.83	.83	.83	.83	.83	.93	.83	.83	.83	.83

APPENDIX TABLE 19

EXPERIMENT III. CLAVICULAR AIR SAC PO_2 GAS TENSIONS (torr)

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

Bird No.	Time (Min)																			
	Control				Ex I				Rest				Ex II				Rest			
	0	30	45	55	2	10	15	20	10	30	60	90	2	10	15	20	10	30	60	90
1	93.7	91.8	93.5	92.1	99.2	100.0	95.8	96.5	91.2	92.0	88.7	95.0	107.8	105.0	100.0	-----	92.5	88.2	90.2	88.0
2	90.0	89.0	92.2	88.0	100.0	107.8	106.0	102.5	93.7	94.8	90.8	90.0	109.3	109.0	106.8	108.0	92.3	96.0	93.8	91.0
3	89.0	90.0	90.8	87.0	102.2	99.0	94.5	96.2	89.3	89.0	86.7	89.0	93.7	99.1	98.0	97.0	91.5	92.2	92.0	93.2
4	95.0	89.8	90.2	87.5	96.9	103.0	102.0	100.0	91.5	89.0	94.5	93.0	103.7	105.0	104.5	103.1	91.7	97.2	93.5	89.8
5	93.2	99.6	99.0	98.0	109.8	110.0	108.0	115.0	104.0	104.8	99.0	99.3	115.5	116.5	110.5	113.5	103.8	103.5	102.0	104.0
$\bar{X}$	92.2	92.0	93.1	90.5	101.6	104.0	101.3	102.0	93.9	93.9	91.9	93.3	106.0	106.9	104.0	104.8	94.4	95.4	94.3	93.2
SE	1.14	1.94	1.57	2.08	1.29	1.29	1.29	1.29	1.29	1.29	1.29	1.29	1.29	1.29	1.29	1.45	1.29	1.29	1.29	1.2[illegible]

APPENDIX TABLE 20

EXPERIMENT III. BODY TEMPERATURE (DEGREES CENTRIGRADE)

AT REST AND DURING EXERCISE

WITH MEANS ($\bar{X}$) AND STANDARD ERROR (SE)

BIRD NO.	TIME (MIN.)																			
	CONTROL				EX I				REST				EX II				REST			
	0	30	45	55	2	10	15	20	10	30	60	90	2	10	15	20	10	30	60	90
1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
2	41.4	41.2	41.5	41.8	42.1	43.0	42.9	42.7	42.0	42.0	42.0	42.2	43.1	43.5	43.5	43.2	42.9	42.5	42.2	42.3
3	40.8	41.0	41.0	41.1	41.5	42.0	42.0	42.0	42.0	42.1	42.5	43.0	43.1	43.2	43.2	43.4	43.2	43.1	43.0	42.8
4	41.0	41.5	41.8	41.8	42.0	42.1	42.1	42.1	42.0	42.1	42.3	42.5	42.8	42.9	42.9	43.0	42.9	42.8	42.8	42.7
5	41.2	41.1	41.1	41.3	42.0	42.6	42.7	42.7	41.9	41.7	42.0	42.1	43.0	43.2	43.1	43.2	42.9	43.0	42.9	42.9
$\bar{X}$	41.1	41.2	41.4	41.5	41.9	42.4	42.4	42.4	42.0	42.0	42.2	42.4	43.0	43.2	43.2	43.2	43.0	42.8	42.7	42.7
SE	.13	.11	.19	.18	.16	.16	.16	.16	.16	.16	.16	.16	.16	.16	.16	.16	.16	.16	.16	.16

CARDIOPULMONARY RESPONSES TO EXERCISE IN THE DUCK

by

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B. A., St. Anselm's College, 1974

AN ABSTRACT OF A MASTER'S THESIS

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The response of the avian cardiopulmonary system to exercise was determined in adult domestic White Pekin ducks (Anas platyrhynchos). In one series of experiments, ten ducks were exercised at three work levels on a treadmill at speeds of 0.9, 1.47, 2.16 km/hr for 20 min with a 90 min rest period following each exercise period. Blood gas and pH analyses were performed on samples simultaneously withdrawn from the brachial artery and right ventricle (as an estimate of mixed venous blood) at predetermined intervals during the experiment. Both arterial PCO_2 ($PaCO_2$) and mixed venous PCO_2 ($P_{\bar{v}}CO_2$) significantly decreased with increased levels of exercise. Arterial pH (pHa) did not change significantly from resting values at any level of exercise. Mixed venous pH ($pH_{\bar{v}}$) decreased at the onset of exercise but returned to near resting values by the end of each exercise period. These measurements indicate that ducks hyperventilate during exercise over and above that required to eliminate the generated CO_2.

In order to further study the ventilatory and cardiovascular responses associated with exercise in the duck, ten additional adult White Pekin ducks were exercised for 20 min on a treadmill (3° incline) at two speeds: 0.9 and 1.47 km/hr. Each exercise period was followed by a 90 min rest period. Both $PaCO_2$ and $P_{\bar{v}}CO_2$ decreased as the running speed increased. $pH_{\bar{v}}$ decreased at the onset of exercise but returned to near resting values by the end of an exercise period. Arterial PO_2 exhibited significant increases at both exercise speeds. Both arterial and mixed venous plasma bicarbonate concentration decreased significantly with each exercise period. Heart rate and systolic and diastolic blood pressure increased significantly during each exercise period. During exercise, tidal volume decreased and respiratory frequency increased. Inspired minute volume markedly increased at the onset of exercise and continued to increase throughout. Body temperature increased 1-2° C during each run. The partial pressure of CO_2 in clavicular air sac gas was determined on an additional five ducks and it decreased at both exercise levels. In these same ducks, $PaCO_2$ also exhibited a sharp fall at both exercise levels while pHa remained unchanged during each run. Because the increased ventilation produced a reduction in $PaCO_2$, it is unlikely that peripheral or central CO_2-sensitive chemoreceptors were responsible for the ventilatory drive; that drive may result from hyperthermia or activity of certain muscle afferents.