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Blood oxygen capacity of birds

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BLOOD OXYGEN CAPACITY IN BIRDS

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ABSTRACT

Avian blood oxygen capacity (BOC: Vol. %) was measured by a modified Roughton - Scholander syringe method with regard to parameters of body weight and sex. Two samples, collected from the Richmond vicinity, were investigated: the domestic pigeon (Columba livia Gmelin) and 25 other bird species.

The results showed that no sexual dimorphism existed in regard to BOC. On the basis of correlation studies, a natural relation was found to occur between BOC and body weight in both samples. This relation was shown to be statistically significant and not due to chance. When BOC/gm. was plotted against body weight on logarithmic scales, it was found to decrease in both samples with increase in body weight. These findings were correlated with the fact that a small bird with a high BOC/gm. can maintain a high metabolic rate.

Blood oxygen capacity per gram body weight in Columba livia was compared with previous vertebrate studies in which a BOC - body weight relation was cited. It was shown by comparison of BOC at 64 grams, that birds have a lower blood oxygen capacity than mammals. Oxygen capacities previously reported for poikilotherms were lower than those of birds.

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INTRODUCTION

Blood oxygen capacity (BOC) is the volume of oxygen contained in an air saturated blood sample. As used in this investigation, oxygen capacity is measured in volumes per cent (Vol. %) which is the number of milliliters of oxygen present in 100 ml. of blood at standard temperature and pressure.

Redfield (1933) has shown that there is a general increase in the oxygen capacity of the blood in the course of the vertebrate evolutionary series. Although the highest blood oxygen capacities occur in mammals and birds, Baldwin (1948) indicates that reptiles and fishes have similar values, but amphibians have higher oxygen capacities close to those found in birds. Homiotherms, however, usually have higher blood oxygen capacities than poikilotherms (Prosser, et al., 1950).

Within the vertebrate classes, considerable variation occurs in BOC from species to species (Redfield, 1933). Burke (1953) has confirmed this variation in mammals and has shown that variation in blood oxygen capacity may be found also within the species. In Rattus norvegicus a BOC - body weight relation was demonstrated by Burke (1957) in which a small rat was found to have a higher blood oxygen capacity per gram body weight than a large one.

In view of this fact, blood oxygen capacity was investigated with regard to body weight and sex in reptiles (Payne, 1957), amphibians (Leftwich, 1958), and fishes (Burke and Woolcott, 1957). These authors showed the existence of a BOC - body weight relation in various vertebrates similar to that found in mammals (Burke, 1957).

Oxygen capacity determinations of avian blood have been published by Drastich (1928), Redfield (1931), Wastl and Leiner (1931), and Christensen and Dill (1935). Values for nine species were reported by these investigators in which blood oxygen capacities ranged from 10.5 to 22 volumes per cent (Table 1).

Since a BOC - body weight relation has been shown to exist in other vertebrates, it was thought that it might also occur in birds. As an approach to this problem, it was decided to investigate blood oxygen capacity in two avian samples with regard to body weight and sex.

Columba livia Gmelin, the domestic pigeon, was chosen as the species for this investigation because it had not been studied before in this manner, information was present in the literature concerning blood studies in this species, and because of the availability of specimens.

The multi-species sample was designed by various collection techniques to contain different birds that could be collected in the Richmond vicinity during early spring. It was believed that blood oxygen capacity, body weight, and sex determinations made on specimens from these samples would upon analysis give some idea of the nature of blood oxygen capacity in birds.

MATERIALS AND METHODS

The procedure used in this study to measure avian blood oxygen capacity was a combination of the syringe method of Roughton and Scholander (1943), Grant's modification of the Roughton - Scholander method (1947), and the procedure of Scholander and van Dam (1956). Each procedure has been compared with a standard manometric method (introduced by Van Slyke, 1924) and found to vary no more than 0.3 Vol. %. The present procedure was run in triplicate on ten pigeons and the results of each sample agreed within 0.2 volumes per cent.

Although oxygen capacity can be measured by several methods, the Grant (1947) modification of the Roughton - Scholander method (1943) was used as it requires only a drop of blood (39.3 cmm.). Excess carbon dioxide is used in this method to extract the oxygen and other gases present in the blood sample. Sodium hydroxide absorbs the carbon dioxide and the residual gas bubble is driven into the graduated capillary of the syringe. Its volume is measured there before and after absorption with alkaline pyrogallol. The difference in the two volumes represents the oxygen content of the reagents and the blood sample. The oxygen content of a previously determined blank (reagents and saline) is subtracted from the oxygen content of the blood sample. The remainder when multiplied by the correction

factor for standard temperature and pressure gives the oxygen capacity of the blood sample in volumes per cent.

When Grant's modification was used in preliminary tests on ducks and pigeons, the blood samples produced viscid ribbons and foams rather than a flocculent precipitate. This resulted in a modification of the Grant procedure used in this investigation.

Scholander and van Dam (1956) reported that proper precipitation of the blood proteins would occur if the acidity of the blood mixture was increased during gas extraction. Certain changes in technique were indicated in their procedure.

However, further changes in the reagents were necessary in the Scholander and van Dam procedure since foams developed occasionally during preliminary tests. In the present study, the acid concentration was increased from 5 ml. to 15 ml. and excellent precipitation occurred in all cases. A urea solution used in the Grant modification (1947) was found to reduce the initial speed of carbon dioxide evolution allowing sufficient time to place the polyethylene plug in the capillary of the syringe analyzer.

A. Apparatus used in the syringe method:

1. A Roughton - Scholander syringe analyzer with 50 capillary divisions.

2. A blood pipette calibrated at 39.3 cmm. and 43.3 cmm.

3. A capillary plug made by fitting a section of polyethylene tubing (I. D. 0.11 in. x 0.024 in.) to a straight pin.

4. A detachable 1 ml. rubber cup which can be fitted to the glass cup of the syringe analyzer.

5. Eight 5 ml. hypodermic syringes with No. 21 needles.

B. Reagents used in the syringe method:

1. Distilled water

2. Isotonic saline. Dissolve 11.7 gm. NaCl in 1 liter of distilled water.

3. Caprylic alcohol

4. Ferricyanide solution. Dissolve 12.5 gm. $K_3Fe(CN)_6$, 3 gm. $KHCO_3$, and 0.5 gm. saponin in 50 ml. of distilled water.

5. Urea. Dissolve 45 gm. urea in 55 ml. of distilled water.

6. Acid sulfate solution. Dissolve 30 gm. anhydrous Na_2SO_4 in 100 ml. of distilled water and add 15 ml. concentrated H_2SO_4.

7. Sodium hydroxide solution. Dissolve 10 gm. NaOH in 50 ml. of distilled water and add 5 gm. anhydrous Na_2SO_4.

8. Pyrogallol solution. Dissolve 20 gm. NaOH in 80 ml. of distilled water. Add 15 gm. of pyrogallol and cover the solution with a layer of mineral oil 2 cm. thick. Dissolve under the oil by stirring with a glass rod.

C. Procedure used in the syringe method:

A mark (designated "upper mark") is placed 5 mm. above the one already on the glass cup of the syringe analyzer. The analyzer is now adjusted to operate with a 39.3 cmm. sample of blood. During the procedure the reagents are added to the analyzer via the 5 ml. hypodermic syringes.

1. The analyzer and blood pipette are mechanically cleaned, washed with detergent and rinsed several times with distilled water and saline. The syringe analyzer is lubricated and filled to the lower mark with saline. The blood pipette is then rinsed with an anticoagulant solution (100 mg. heparin per 15 ml. 0.20 M NaCl).
2. A 39.3 cmm. heparinized blood sample is added to the analyzer from the pipette. The syringe plunger is withdrawn until the blood sample meets the bottom of the cup.
3. Two drops of caprylic alcohol are added to the blood sample and withdrawn into the barrel of the syringe to reduce the development of transverse blood films.
4. The plunger is withdrawn so that approximately 1 ml. of air is introduced into the syringe. Aeration of the blood sample is accomplished by rotating the analyzer on its long axis and occasionally at right angles to spread a small layer of blood on and over the inside of the barrel. Once a minute during five minutes a new volume of air is introduced into the syringe.

5. The blood sample is pushed up to the top of the capillary and the analyzer cup is filled to the upper mark with ferricyanide solution. This is withdrawn into the syringe to the bottom of the cup. Saponin in the ferricyanide solution promotes lysis of the erythrocyte walls and releases the contained hemoglobin. The hemoglobin of the blood sample is then converted by potassium ferricyanide to methemoglobin which is incapable of combining reversibly with molecular oxygen. Potassium bicarbonate in the solution provides the source of carbon dioxide during gas extraction.
6. The analyzer cup is filled to the upper mark with urea. This is withdrawn into the syringe to the bottom of the cup to temporarily separate the ferricyanide solution from the acid sulfate.
7. The analyzer cup is filled to the upper mark with acid sulfate solution. This is withdrawn into the syringe but not quite to the bottom of the cup. The polyethylene stopper is quickly plugged into the capillary of the syringe. The remaining acid solution provides a liquid seal for the self-retained stopper.
8. The analyzer is shaken for two minutes during which carbon dioxide is evolved in an H_2SO_4 - Na_2SO_4 buffered system. The blood sample now appears a brown flocculent precipitate.
9. The pressure in the syringe barrel is adjusted to

atmospheric by gradually withdrawing the plunger at the same time cautiously removing the stopper to maintain the gas bubble in the syringe.

10. The rubber cup is attached to the glass cup of the analyzer and 1 ml. of sodium hydroxide solution is added. This is withdrawn into the syringe barrel to absorb the excess carbon dioxide.

11. The gas bubble, reduced in volume, is pushed into the graduated capillary by careful manipulation of the plunger. With the rubber cup removed, the analyzer is placed in a room temperature water bath for a 30 second equilibration period.

12. The gas bubble, containing oxygen, carbon monoxide, and nitrogen from the blood and reagents, is measured in length by the divisions on the capillary. This volume is recorded as V_1.

13. The contents of the analyzer cup are removed from the bottom of the cup and it is filled to the upper mark with pyrogallol solution. Pyrogallol is drawn into the capillary absorbing the oxygen contained in the bubble. When the bubble reaches constant length it is recorded as V_2.

14. The procedure must be repeated using 43.3 cmm. of saline to determine the oxygen content of the reagents and that physically dissolved in the blood (Sendroy, et. al., 1934).

15. Blood oxygen capacity is calculated by using the following formulas:

Saline blank	Blood sample
$c = (V_1 - V_2)\ f$	$BOC = (V_1 - V_2 - c)\ f$

c = Oxygen capacity of the saline blank.

f = STP conversion factor (Peters and Van Slyke, 1932) based on the temperature of operation and the barometric reading corrected for brass scale expansion (Hodgman, 1957).

BOC = Oxygen capacity of the blood sample in volumes per cent.

D. Experimental procedure:

Birds were obtained in various ways. Specimens were removed from nests, trapped with nets or wounded with 0.22 cal. rifle, 0.22 cal. carbon dioxide rifle, 0.410 cal., 20 ga., and 12 ga. shotguns.

Blood was withdrawn directly from the heart into heparinized syringes and transferred by pipette to the Roughton - Scholander syringe for oxygen capacity measurement. After the determination, the specimen was weighed to the nearest gram and sexed according to Hyman (1942). Species identification was facilitated by Peterson (1947) and Brodkorb (Blair, et al., 1957). Blood oxygen capacity, body weight, blood oxygen capacity per gram body weight, and sex were recorded for each specimen. Statistical analyses were made according to Arkin and Colton (1956) and Simpson, Roe and Lewontin (1960).

RESULTS

In Table 2, 26 species (123 specimens) collected in the Richmond vicinity are listed according to their scientific names. Blood oxygen capacity, body weight, blood oxygen capacity per gram of body weight, and sex obtained from each specimen are shown in Tables 3 and 5. Data for Columba livia Gmelin (56 individuals) are arranged in Table 3 with weight in ascending order. Specimens from 25 other avian species (67 individuals) are listed according to the taxonomic scheme of Brodkorb (Blair, et al., 1957).

Blood oxygen capacity and body weight for immature, mature, male, and female groups are summarized for C. livia in Table 4.

On the basis of adult weight, a sampling validity of 95% was indicated by mean weight (306 gm.) plus or minus two standard deviations (120 gm.). The actual weight range was 182 - 464 gm., whereas the 95% range was 186 - 426 gm.

A statistically significant difference was shown to exist between the mean blood oxygen capacities of the immature group (9.3 Vol. %) and the mature group (13.3 Vol. %). This was indicated by three times the standard error of the difference between the means (2.1 Vol. %) which was less than the arithmetic difference between the means (4.0 Vol. %). When male and female oxygen capacities (13.8 and 12.7 Vol. % respectively) were compared on this basis, no significant difference was found to occur (A. D. m. = 1.1 Vol. %; 3 x S. E. d. = 3.3 Vol. %).

In the multi-species sample, mean blood oxygen capacity was 12.3 volumes per cent (standard deviation 2.5 Vol. %). Oxygen capacity for males (12.1 Vol. %) was somewhat lower than that for females (13.3 Vol. %). Compared with C. livia (BOC: 13.3, S. D. = 2.5 Vol. %), the mean blood oxygen capacity of the multi-species sample was lower (BOC: 12.3, S. D. = 2.5 Vol. %). With regard to the weight range of samples in the 25 species (12 - 3,710 gm.), it was much greater than that found in pigeons (11 - 464 gm.).

A natural relation between log BOC and log body weight was shown for C. livia. A correlation coefficient of 0.50 for pigeons was shown not to occur by chance ($p = 0.001$). Similarly, a correlation coefficient of 0.33 ($p = 0.01$) was indicated in the multi-species sample.

For each specimen, blood oxygen capacity per gram of body weight was plotted against corresponding body weight on logarithmic scales. Those plotted for C. livia are shown in Figure 1 and those for the multi-species sample are shown in Figure 2. In both graphs, the regression lines show that blood oxygen capacity per gram of body weight decreases with increase in body weight.

The regression lines of Figures 1 and 2 were plotted from equations derived from the data by the method of least squares (Arkin and Colton, 1956; Simpson, et al., 1960).

The following equations were obtained:

1. Columba livia;

$$BOC/gm. = (5)(Wt.\ in\ gm.)^{-0.85}$$

2. Multi-species sample;

$$BOC/gm. = (10)(Wt.\ in\ gm.)^{-0.96}$$

Procedures for determining these equations and plotting the regression lines are provided in the Appendix.

DISCUSSION

The results in Table 3 show that sexually immature specimens as well as sexually mature adults of Columba livia were collected in this study. The immature specimens, more difficult to obtain, were sparsely scattered within a weight range of 11 to 256 grams. It was found, however, that the weight range of the adults (Table 4) was greater than the 95% range as indicated by mean adult weight plus or minus two times the standard deviation (306 = 120 gm.). On the basis of adult weight a statistically valid sample was thus obtained from Columba livia. A significant difference was shown to exist between mean oxygen capacities of immature and mature pigeons. It was found that three times the standard error of the difference between the means (2.1 Vol. %) was half as great as the arithmetic difference between the means (4.0 Vol. %). Although a difference occurred between the mean oxygen capacities of males and females (1.1 Vol. %), it was not statistically significant (3 x S. E. d. = 3.3 Vol. %).

Differences in oxygen capacities have been indicated in other investigations in young and adult birds. Rostorfer and Rigdon (1946) have shown that the oxygen capacity of young ducks increases with age from the time of hatching until maturity. Earlier, Hall (1934) found that hemoglobin obtained from chick embryos had a greater affinity for oxygen than hemoglobin from

the mature fowl. Christensen and Dill (1935) suggested that two types of hemoglobin might be present in avian blood accounting for the differences in oxygen capacity and differences in the oxygen affinity of young and adult bird hemoglobins. The presence of dual hemoglobins in ducks, chickens, and pigeons has been confirmed by electrophoretic studies (Johnson, et al., 1955 and Saha, et al., 1957). It was found that the proportions of these hemoglobins in avian blood varied from one species to another.

The multi-species sample (Table 5) was composed of avian species collected in the Richmond vicinity during early spring. Most of the specimens obtained weighed between 12 and 150 grams; however some weights were sparsely scattered between 200 and 3,710 grams. The weight range of the multi-species sample (12 - 3,710 gm.) was found to be 8 times greater than that for Columba livia (11 - 464 gm.). Large standard deviations calculated for these samples showed that statistical comparisons of mean weights were not valid. Mean blood oxygen capacity (12.3 Vol. %), on the other hand, was lower for this sample in contrast to that of C. livia (13.3 Vol. %). On the basis of three times the standard error of the difference between the two means, this value was not significantly lower. In the multi-species sample no significant difference occurred between the mean oxygen capacities of males and females. This was also found to be true in pigeons.

The data showed that there was a general tendency for BOC to increase with increasing body weight in Columba livia (Table 3). Arithmetic graphs of BOC versus body weight, when originally plotted, confirmed the existence of a curvilinear trend. The relation of BOC and body weight proved to be logarithmic since a straight regression line was indicated when these parameters were plotted on logarithmic scales. In pigeons, the correlation coefficient of log BOC vs. log body weight was 0.50. The probability was less than one in a thousand ($p = 0.001$) that this relation occurred in the sample by chance. A logarithmic relation between BOC and body weight was also found to occur in the multi-species sample. The correlation coefficient in this sample was 0.33 with a probability of chance occurrence less than one in a hundred ($p = 0.01$). The lower correlation coefficient in the multi-species sample was expected since the BOC (BOC: 6.3 - 18.6 Vol. %; body weight: 12 - 3,710 gm.) did not continually increase with an increase in body weight as it did in C. livia (BOC: 5.1 - 7.5 Vol. %; 11 - 464 gm.). The results of the correlation study suggest that a natural relation exists between blood oxygen capacity and body weight in the avian populations from which these samples were obtained.

In the studies of Burke (1957), Burke and Woolcott (1957), Payne (1957), and Leftwich (1958), the BOC - body weight relation was analyzed graphically by plotting BOC/gm. vs. body weight,

which was also done in this study for comparison with these investigations. Logarithmic scales, however, were used in Figures 1 and 2 so a straight regression line would show the trend indicated by the scattered points. Figure 1 shows a log log plot of blood oxygen capacity per gram body weight versus body weight in a bird species, Columba livia. In Figure 2, BOC/gm. vs. body weight is plotted for representatives of 25 avian species.

For each sample, a regression line was plotted using an equation derived from the data by the method of least squares (Appendix). The following regression equations were used:

1. Columba livia:

$$\text{BOC/gm.} = (5)(\text{Wt. in gm.})^{-0.85}$$

2. Multi-species sample:

$$\text{BOC/gm.} = (10)(\text{Wt. in gm.})^{-0.96}$$

In the equation for C. livia, the exponent -0.85 represents the slope (b_y) of the line, whereas the constant 5 indicates the BOC of a pigeon weighing 1 gram. In contrast, the exponent and constant are greater in the multi-species regression equation. This difference is due to a greater decrease in BOC/gm. (0.53. - 0.0040 Vol. %/gm.) with increase in body weight (12 - 3,710 gm.) than that occurring in Columba livia (BOC/gm.: 0.46 - 0.029 Vol. %/gm.; body weight: 11 - 464 gm.).

The regression equation for C. livia may be used to predict the average BOC/gm. for a pigeon of known weight. Procedures used for computation may be found in the Appendix. From the BOC/gm. obtained, blood oxygen capacity can be calculated by multiplying BOC/gm. by the body weight of the pigeon. Also, BOC/gm. at a given weight of pigeon may be read directly from the graph in Figure 1 by means of the straight regression line.

It is evident from the graph in Figure 1 that blood oxygen capacity per gram decreases with increasing body weight. No significant difference occurred in this trend with regard to sex or condition of gonads. However, the mean BOC/gm. of immature pigeons (0.99 Vol. %/gm.) was significantly higher than that of the mature group (0.043 Vol. %/gm.). This was expected since mean BOC and mean body weight were lower than those of the adults. Accordingly, the BOC/gm. for males and females was essentially the same (0.044 and 0.043 Vol. %/gm. respectively) since mean BOC and mean weight were not greatly different.

Brody (1945) has shown that basal metabolism (cal./day) varies with body weight in birds. Since basal heat production is an indicator of metabolic rate (cal./gm./day), blood oxygen capacity per gram body weight is important in that the blood transports oxygen for the respiratory function. The regression lines of Figures 1 and 2 show that a small bird has a higher blood oxygen capacity per unit body weight than a large one. Thus, the small bird is able to maintain a higher metabolic rate by virtue

of a higher oxygen capacity per gram. Burke (1957) has shown a similar mechanism with regard to small mammals in which high oxygen consumption rate, high blood volume per gram and high blood oxygen capacity per gram enable the occurrence of a high metabolic rate.

In the investigation of blood oxygen capacity in birds, several facts were found to be similar to those demonstrated in mammal studies (Rattus norvegicus) by Burke (1957); fishes (Lepomis macrochirus and Pomoxis nigromaculatus), Burke and Woolcott (1957); reptiles (Chrysemys picta and Terrapene carolina), Payne (1957); and amphibians (Rana catesbiana, Rana clamitans, and Rana pipiens), Leftwich (1958). In all of these studies, blood oxygen capacity per gram body weight was found to decrease with increasing body weight. No significant difference was found in this pattern with regard to sex or condition of gonads. Also, blood oxygen capacity was found to be lower in young mammals in contrast to that of adults (Burke, 1953). This study supports the findings of the previous authors in all vertebrate classes.

The BOC - body weight relation was of particular interest in birds since it was not known what increase to expect in BOC with increase in body weight (Table 1). On the basis of the principle of similitude (Giese, 1957), the mass of bone, cartilage, and fibrous connective tissue increases disproportionally as the animal increases in size. Such tissue is relatively inert metabolically and contributes little to metabolic

rate (Zeuthen, 1953). As there are structural adaptations in birds enabling flight such as feathers, bones with air spaces, and air sacs (Blair, et al., 1957), it was thought that total body weight might increase disproportionally with increase in blood oxygen capacity. Blood oxygen capacity per gram body weight in Columba livia was compared with the previous vertebrate studies in which a BOC - body weight relation was cited. Comparison was accomplished by obtaining the blood oxygen capacities and body weights for each specimen in the eight species reported. Blood oxygen capacity was divided by body weight to obtain BOC/gm. This was plotted against body weight for each species on logarithmic scales. Regression lines, representing the trend of the scattered points, were determined by inspection. When the regression lines were plotted on the same graph with that of C. livia, it was found that the weight ranges for the nine species overlapped at 64 grams.

In Table 6, BOC/gm. at 64 grams is listed for representatives in each vertebrate class. Blood oxygen capacities for these species at 64 grams were compared with oxygen capacities reported for vertebrates by Baldwin (1948) at unspecified weights. From this comparison it was shown that birds have a lower blood oxygen capacity than mammals; however, oxygen capacities which have been reported for the poikilotherms (reptiles, amphibians, and fishes) are lower than those of homoiotherms.

SUMMARY

1. Avian blood oxygen capacity (BOC: Vol. %) was measured by a modified Roughton - Scholander syringe method with regard to body weight (gm.) and sex. Although BOC had been determined before in birds, it was not analyzed in reference to sex and body weight parameters (Table 1). Two samples, collected from the Richmond vicinity, were investigated (Table 2): the domestic pigeon, Columba livia Gmelin, (Tables 3 and 4) and 25 other bird species (Table 5).
2. Blood oxygen capacity in sexually immature pigeons (9.3 Vol. %) was significantly lower than that of the adults (13.3 Vol. %). In both C. livia and the multi-species sample no significant difference occurred between the mean blood oxygen capacities of male and female specimens.
3. A natural relation between log BOC and log body weight was shown for C. livia. A correlation coefficient of 0.50 for pigeons was shown not to occur by chance ($p = 0.001$). Similarly, a correlation coefficient of 0.33 ($p = 0.01$) was indicated in the multi-species sample.
4. On logarithmic scales (Figures 1 and 2), avian blood oxygen capacity per gram body weight was found to decrease with increasing body weight. Thus, a small bird with a high BOC/gm. can maintain a high metabolic rate.

5. Blood oxygen capacity per gram body weight in Columba livia was compared with previously reported vertebrate studies in which a BOC - body weight relation was cited (Table 6). It was shown by comparison of BOC at 64 grams, that birds have a lower blood oxygen capacity than mammals. Oxygen capacities for poikilotherms were lower than those of homoiotherms.

Table 1.

Avian Blood Oxygen Capacities Published in Available Literature

	Species	Oxygen Capacity (Vol. %)	Method	Authority	Date
1.	chicken	10.5	Van Slyke	Christensen & Dill	1935
2.	crow	17	Van Slyke	Wastl & Leiner	1931
		22	Hemoglobin	Drastich	1928
3.	duck	12.3	Van Slyke	Christensen & Dill	1935
		17	Van Slyke	Wastl & Leiner	1931
4.	goose	19.8	Van Slyke	Wastl & Leiner	1931
5.	owl	19	Van Slyke	Wastl & Leiner	1931
6.	pigeon	20	Van Slyke	Wastl & Leiner	1931
		21	Hemoglobin	Drastich	1928
7.	serin	14	Hemoglobin	Drastich	1928
8.	sparrow	14.5	Van Slyke	Christensen & Dill	1935
		14.5	Hemoglobin	Drastich	1928
9.	surf scooter	22	Van Slyke	Redfield	1931

Table 2.

Avian Species Collected in This Study

	Species:	No.
1.	Anas platyrhyncos Linnaeus	7
2.	Gallus gallus Linnaeus	4
3.	Chadrius vociferus Linnaeus	2
4.	Columba livia Gmelin	56
5.	Colaptes auratus (Linnaeus)	2
6.	Melanerpes carolinus (Linnaeus)	2
7.	Sayornis phoebe (Latham)	2
8.	Corvus ossifragus Wilson	2
9.	Corvus brachyrhyncos Brehm	2
10.	Cyanocitta cristata Linnaeus	2
11.	Baeolophus bicolor (Linnaeus)	2
12.	Mimus polyglottis (Linnaeus)	3
13.	Dumetella carolinensis Linnaeus	2
14.	Turdus migratorius Linnaeus	3
15.	Lanius ludovicianus Linnaeus	2
16.	Sturnus vulgaris Linnaeus	4
17.	Molothrus ater (Boddaert)	3
18.	Agelaius phoeniceus (Linnaeus)	2
19.	Cassidix mexicanus (Gmelin)	4
20.	Pyrrhuloxia cardinalis (Linnaeus)	3
21.	Passer domesticus (Linnaeus)	2
22.	Piplo erythrophthalmus Linnaeus	2
23.	Passerculus sandwichensis (Gmelin)	3
24.	Melospiza melodia (Wilson)	2
25.	Spizella pusilla (Wilson)	2
26.	Junco hyemalis (Linnaeus)	3
		123

Table 3.

BLOOD OXYGEN CAPACITY IN *COLUMBA LIVIA* GMELIN

BOC (Vol. %)	Body Weight (gm.)	BOC / gm.	Sex*
5.1	11	0.46	I
6.9	11	0.63	I
7.2	11	0.65	I
10.0	13	0.77	I
6.5	13	0.50	I
7.3	15	0.49	I
6.1	18	0.34	I
8.0	19	0.42	I
9.1	25	0.36	I
7.6	27	0.28	I
7.9	34	0.23	I
6.3	38	0.17	I
8.7	40	0.22	I
11.4	49	0.23	I
9.6	51	0.19	I
7.7	54	0.14	I
7.9	58	0.14	I
6.4	67	0.095	I
9.2	77	0.12	I
13.0	81	0.16	I
8.1	84	0.096	I

* I = sexually immature

Table 3. (Cont'd.)

BLOOD OXYGEN CAPACITY IN *COLUMBA LIVIA* GMELIN

BOC (Vol. %)	Body Weight (gm.)	BOC / gm.	Sex*
9.1	103	0.088	I
8.2	105	0.078	I
12.0	119	0.10	I
8.9	124	0.071	I
8.5	152	0.056	I
11.3	155	0.073	I
7.5	166	0.045	I
11.0	182	0.060	F
13.0	209	0.062	I
10.0	215	0.046	I
13.1	221	0.059	I
13.5	221	0.061	M
13.7	226	0.061	I
15.3	242	0.063	I
15.2	256	0.059	I
9.4	260	0.036	F
14.4	262	0.055	M
17.5	268	0.065	F
14.1	270	0.052	F
17.4	270	0.064	M
15.4	272	0.057	M

* I = sexually immature

M = male

F = female

Table 3. (Cont'd.)

BLOOD OXYGEN CAPACITY IN COLUMBA LIVIA GMELIN

BOC (Vol. %)	Body Weight (gm.)	BOC / gm.	Sex*
11.1	274	0.041	F
13.0	288	0.045	F
13.3	292	0.045	F
11.5	304	0.038	M
15.3	316	0.048	M
9.2	324	0.028	M
13.2	327	0.040	F
9.6	332	0.029	F
12.4	338	0.037	M
15.2	343	0.044	M
14.4	364	0.039	M
10.6	373	0.028	F
17.2	385	0.045	F
13.3	464	0.029	M

*

M = male

F = female

Abbreviations Used in Table 4.

BOC = Blood oxygen capacity in volumes per cent.

Wt. = Body weight in grams.

No. = Number of specimens.

Max. = Maximum value.

Min. = Minimum value.

S. D. = Standard deviation.

2 x S. D. = Two times the standard deviation.

S. E. m. = Standard error of the mean.

A. D. m. = Arithmetic difference between two means.

S. E. d. = Standard error of the difference between two means.

3 x S. E. d. = Three times the standard error of the difference between two means.

Table 4.

Columba livia Gmelin

Immature No. 34	BOC	Wt.
Max.	15.3	256
Min.	5.1	11
Mean	9.3	91
S. D.	2.6	--
S. E. m.	0.45	--

Mature No. 22	BOC	Wt.
Max.	17.5	464
Min.	9.2	182
Mean	13.3	306
S. D.	2.5	60
S. E. m.	0.53	--
2 x S. D.	----	120

BOC Immature vs. Mature	
A. D. m.	4.0
S. E. d.	0.7
3 x S. E. d.	2.1

Male No. 11	BOC	Wt.
Max.	17.4	464
Min.	9.2	221
Mean	13.8	316
S. D.	2.2	---
S. E. m.	0.66	---

Female No. 11	BOC	Wt.
Max.	17.5	385
Min.	9.4	182
Mean	12.7	296
S. D.	2.8	---
S. E. m.	0.85	---

BOC Male vs. Female	
A. D. m.	1.1
S. E. d.	1.1
3 x S. E. d.	3.3

Table 5.

BLOOD OXYGEN CAPACITY IN VARIOUS BIRDS

	BOC (Vol. %)	Body Weight (gm.)	BOC / gm.	Sex
Anseriformes Anatidae				
Anas platyrhyncos Linnaeus	15.4	926	0.017	F
Anas platyrhyncos Linnaeus	11.8	1390	0.0084	F
Anas platyrhyncos Linnaeus	17.4	2360	0.0073	F
Anas platyrhyncos Linnaeus	13.3	2580	0.0051	-
Anas platyrhyncos Linnaeus	9.2	2870	0.0032	-
Anas platyrhyncos Linnaeus	8.8	3100	0.0028	-
Anas platyrhyncos Linnaeus	14.8	3710	0.0040	F
Galliformes Phasianidae				
Gallus gallus Linnaeus	11.0	40	0.28	I
Gallus gallus Linnaeus	8.4	44	0.19	I
Gallus gallus Linnaeus	12.3	46	0.27	I
Gallus gallus Linnaeus	13.2	2730	0.0048	F
Charadriiformes Charadriidae				
Charadrius vociferus Linnaeus	12.8	80	0.16	F
Charadrius vociferus Linnaeus	9.7	98	0.099	M

Table 5. (Cont'd)

BLOOD OXYGEN CAPACITY IN VARIOUS BIRDS

	BOC (Vol.%)	Body Weight (gm.)	BOC / gm.	Sex
Piciformes				
Picidae				
Colaptes auratus (Linnaeus)	18.6	119	0.16	M
Colaptes auratus (Linnaeus)	15.4	123	0.13	M
Melanerpes carolinus (Linnaeus)	13.0	70	0.19	M
Melanerpes carolinus (Linnaeus)	12.3	73	0.17	M
Passeriformes				
Tyrannidae				
Sayornis phoebe (Latham)	6.9	18	0.38	M
Sayornis phoebe (Latham)	9.0	19	0.47	M
Corvidae				
Corvus ossifragus Wilson	11.1	226	0.049	M
Corvus ossifragus Wilson	14.9	315	0.047	F
Corvus brachyrhyncos Brehm	19.4	462	0.042	F
Corvus brachyrhyncos Brehm	16.0	585	0.027	M
Cyanocitta cristata Linnaeus	12.3	84	0.15	M
Cyanocitta cristata Linnaeus	12.3	86	0.14	M

Table 5. (Cont'd)

BLOOD OXYGEN CAPACITY IN VARIOUS BIRDS

Passeriformes Paridae	BOC (Vol. %)	Body Weight (gm.)	BOC gm.	Sex
Baeolophus bicolor (Linnaeus)	12.9	22	0.59	M
Baeolophus bicolor (Linnaeus)	14.3	24	0.60	M
Mimidae				
Mimus polyglottis (Linnaeus)	13.2	57	0.23	M
Mimus polyglottis (Linnaeus)	15.4	60	0.26	M
Mimus polyglottis (Linnaeus)	14.3	61	0.23	F
Dumetella carolinensis Linnaeus	11.8	35	0.34	M
Dumetella carolinensis Linnaeus	8.8	38	0.23	M
Turdidae				
Turdus migratorius Linnaeus	14.9	78	0.19	F
Turdus migratorius Linnaeus	11.6	79	0.15	F
Turdus migratorius Linnaeus	16.2	91	0.18	F
Laniidae				
Lanius ludovicianus Linnaeus	12.9	51	0.25	M
Lanius ludovicianus Linnaeus	11.6	53	0.22	M

Table 5. (Cont'd)

BLOOD OXYGEN CAPACITY IN VARIOUS BIRDS

Passeriformes Sturnidae	BOC (Vol. %)	Body Weight (gm.)	BOC gm.	Sex
Sturnus vulgaris Linnaeus	10.2	80	0.13	F
Sturnus vulgaris Linnaeus	10.7	82	0.13	M
Sturnus vulgaris Linnaeus	11.9	88	0.13	M
Sturnus vulgaris Linnaeus	12.7	89	0.14	M
Icteridae				
Molothrus ater (Boddaert)	12.3	48	0.26	F
Molothrus ater (Boddaert)	11.6	51	0.23	M
Molothrus ater (Boddaert)	11.8	53	0.22	M
Agelaius phoeniceus (Linnaeus)	15.2	60	0.25	M
Agelaius phoeniceus (Linnaeus)	17.9	62	0.29	M
Cassidix mexicanus (Gmelin)	10.4	100	0.10	F
Cassidix mexicanus (Gmelin)	12.2	121	0.10	F
Cassidix mexicanus (Gmelin)	17.0	131	0.13	F
Cassidix mexicanus (Gmelin)	8.6	133	0.065	M

Table 5. (Cont'd)

BLOOD OXYGEN CAPACITY IN VARIOUS BIRDS

Passeriformes Thraupidae	BOC (Vol. %)	Body Weight (gm.)	BOC/gm.	Sex
Pyrrhuloxia cardinalis (Linnaeus)	12.2	41	0.30	M
Pyrrhuloxia cardinalis (Linnaeus)	10.8	43	0.25	M
Pyrrhuloxia cardinalis (Linnaeus)	11.6	45	0.26	M
Ploceidae				
Passer domesticus (Linnaeus)	9.4	30	0.31	F
Passer domesticus (Linnaeus)	10.8	31	0.35	M
Fringillidae				
Piplo erythrophthalmus Linnaeus	12.0	42	0.29	F
Piplo erythrophthalmus Linnaeus	13.6	44	0.31	M
Passerculus sandwichensis (Gmelin)	12.9	27	0.48	F
Passerculus sandwichensis (Gmelin)	13.0	32	0.41	M
Passerculus sandwichensis (Gmelin)	11.2	35	0.32	M
Melospiza melodia (Wilson)	11.0	21	0.52	M
Melospiza melodia (Wilson)	12.6	23	0.55	M

Table 5. (Cont'd)

BLOOD OXYGEN CAPACITY IN VARIOUS BIRDS

Passeriformes Fringillidae	BOC (Vol. %)	Body Weight (gm.)	BOC gm.	Sex*
Spizella pusilla (Wilson)	6.3	12	0.53	M
Spizella pusilla (Wilson)	8.8	13	0.68	F
Junco hyemalis (Linnaeus)	9.0	19	0.47	M
Junco hyemalis (Linnaeus)	10.3	20	0.51	F
Junco hyemalis (Linnaeus)	12.4	21	0.59	M

* I = Sexually Immature

M = Male

F = Female

Table 6.

A Comparison of Blood Oxygen Capacity in Vertebrate Classes

Class	BOC (Vol. %)*	BOC (Vol. %)**	Authority
Mammalia	25	14.1	Burke, 1957
Aves	18.5	9.6	Powell, 1961
Reptilia	9	5.0	Payne, 1957
Amphibia	12	8.5	Leftwich, 1958
Pisces[1]	9	8.4	Burke and Woolcott, 1957

---

* Unspecified weight (Baldwin, 1948)

** Weight = 64 grams

1. After Baldwin, 1948

Fig. 1. The Relation Between Blood Oxygen Capacity (Vol. %) per Gram Body Weight and Body Weight (gm.) in *Columba livia* Gmelin.

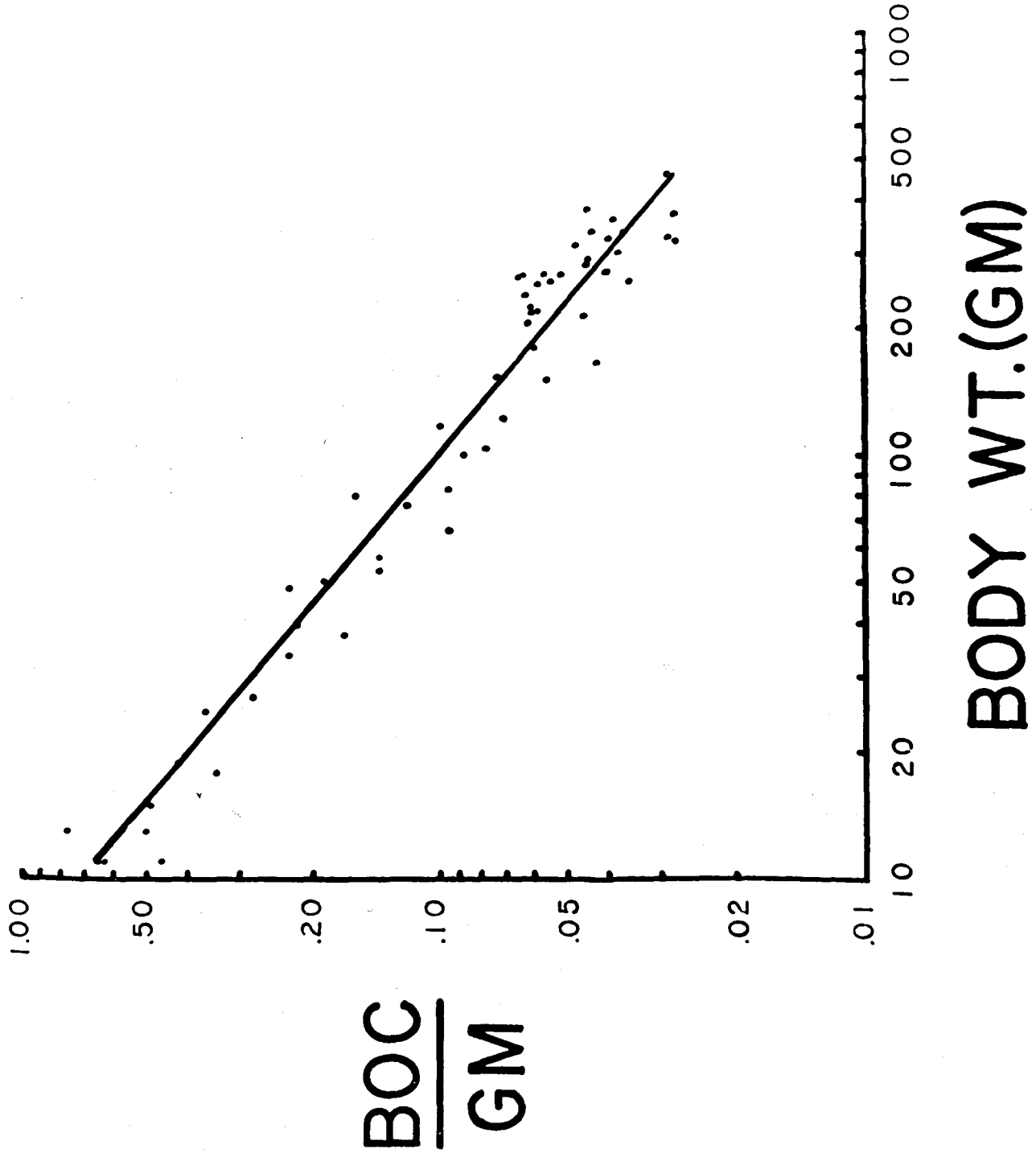
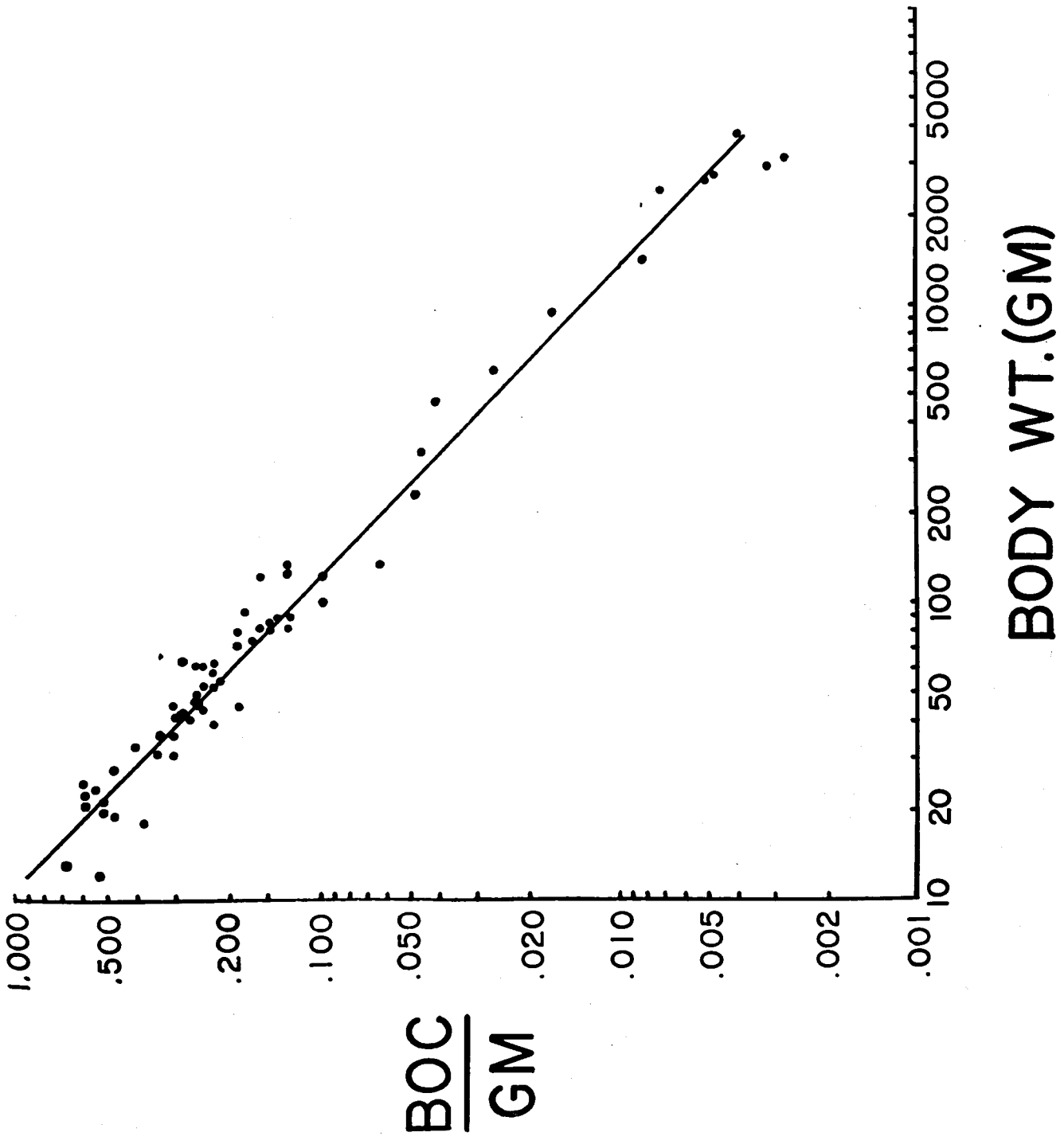

BOC/GM
1.00
.50
.20
.10
.05
.02
.01
10
20
50
100
200
500
1000
BODY WT.(GM)

Fig. 2. The Relation Between Blood Oxygen Capacity (Vol. %) per Gram Body Weight and Body Weight (gm.) in the Multi-species Sample.


BOC/GM
1.000
.500
.200
.100
.050
.020
.010
.005
.002
.001
10
20
50
100
200
500
1000
2000
5000
BODY WT.(GM)

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VITA

James R. Powell was born on December 29, 1937 in Pittsburgh, Pa. He was educated in the elementary schools of Windber and Huntingdon, Pa. In 1955 he graduated from Huntingdon High School and entered Juniata College at Huntingdon the following September. During the next four years he majored in biology and received the B. S. degree in 1959. During the summer of 1959 he attended the Mountain Lake Biological Station of the University of Virginia where he began his graduate studies in biology.

In September of 1959 he entered the University of Richmond to begin on the Master of Arts degree. During the first year he received an assistantship at the Department of Biology and gained experience in teaching. For the summer of 1960 he was appointed technical assistant to Dr. J. D. Burke of the Department of Biology, University of Richmond. The second year he was honored with a Williams Fellowship and also received a Departmental assistantship. Presently he is a candidate for the Master of Arts degree in June of 1961. He plans to continue his studies in biology at the Virginia Polytechnic Institute where he will begin work on the doctorate in July of 1961.

James R. Powell is a member of the Virginia Academy of Science and the Beta Theta chapter of Beta Beta Beta.

APPENDIX

Correlation of log BOC and log Wt.

Columba livia:

1.) $r = \frac{\Sigma xy}{\sqrt{(\Sigma x^2)(\Sigma y^2)}}$; (Simpson, Roe, and Lewontin, 1960)

Y = log BOC
X = log Wt.

2.) $\Sigma xy = \Sigma XY - \frac{(\Sigma X)(\Sigma Y)}{n}$

$\Sigma XY - \frac{(\Sigma X)(\Sigma Y)}{n} = 1.688$

$\Sigma XY = 119.104$
$\Sigma X = 115.597$
$\Sigma Y = 56.881$
$(\Sigma X)(\Sigma Y) = 6,575.273$
$\frac{(\Sigma X)(\Sigma Y)}{n} = 117.416$
$n = 56$

$\Sigma xy = 1.688$

3.) $\Sigma x^2 = \Sigma X^2 - \frac{(\Sigma X)^2}{n}$

$\Sigma X^2 - \frac{(\Sigma X)^2}{n} = 11.806$

$\Sigma X^2 = 250.425$
$\Sigma X = 115.597$
$(\Sigma X)^2 = 13,362.667$
$\frac{(\Sigma X)^2}{n} = 238.619$
$n = 56$

$\Sigma x^2 = 11.806$

Correlation of log BOC and log Wt.

Columba livia:

4.) $\Sigma y^2 = \Sigma Y^2 - \frac{(\Sigma Y)^2}{n}$

$\Sigma Y^2 = 58.758$

$\Sigma Y = 56.881$

$(\Sigma Y)^2 = 3{,}235.448$

$\frac{(\Sigma Y)^2}{n} = 57.776$

$n = 56$

$\Sigma Y^2 - \frac{(\Sigma Y)^2}{n} = 0.982$

$\Sigma y^2 = 0.982$

5.) $r = \frac{\Sigma xy}{\sqrt{(\Sigma x^2)(\Sigma y^2)}}$

$\Sigma x^2 = 11.806$

$\Sigma y^2 = 0.982$

$(\Sigma x^2)(\Sigma y^2) = 11.593$

$\sqrt{(\Sigma x^2)(\Sigma y^2)} = 3.405$

$\Sigma xy = 1.688$

$\frac{\Sigma xy}{\sqrt{(\Sigma x^2)(\Sigma y^2)}} = 0.50$

$r = 0.50$

P = less than 0.001 (Simpson, Roe, and Lewontin, 1960): p. 426 Table V)

Correlation of log BOC and log Wt.

Multi-species sample:

1.) $R = \dfrac{\Sigma xy}{\sqrt{(\Sigma x^2)(\Sigma y^2)}}$; (Simpson, Roe, and Lewontin, 1960)

Y = log BOC

X = log Wt.

2.) $\Sigma xy = \Sigma XY - \dfrac{(\Sigma X)(\Sigma Y)}{n}$

$\Sigma XY = 141.282$

$\Sigma X = 129.455$

$\Sigma Y = 72.442$

$(\Sigma X)(\Sigma Y) = 9{,}377.979$

$\dfrac{(\Sigma X)(\Sigma Y)}{n} = 139.970$

$n = 67$

$\Sigma xy = 1.312$

$\Sigma XY - \dfrac{(\Sigma X)(\Sigma Y)}{n} = 1.312$

$\Sigma x^2 = \Sigma X^2 - \dfrac{(\Sigma X)^2}{n}$

$\Sigma X^2 = 275.133$

$\Sigma X = 129.455$

$(\Sigma X)^2 = 16{,}758.597$

$\dfrac{(\Sigma X)^2}{n} = 250.128$

$n = 67$

$\Sigma x^2 = 25.005$

$\Sigma X^2 - \dfrac{(\Sigma X)^2}{n} = 25.005$

Correlation of log BOC and log Wt.

Multi-species sample:

4.) $\Sigma y^2 = \Sigma Y^2 - \frac{(\Sigma Y)^2}{n}$

$\Sigma Y^2 = 78.940$

$\Sigma Y = 72.442$

$(\Sigma Y)^2 = 5,247.843$

$\frac{(\Sigma Y)^2}{n} = 78.326$

$n = 67$

$\Sigma y^2 = 0.614$

$\Sigma Y^2 - \frac{(\Sigma Y)^2}{n} = 0.614$

5.) $r = \frac{\Sigma xy}{\sqrt{(\Sigma x^2)(\Sigma y^2)}}$

$\Sigma x^2 = 25.005$

$\Sigma y^2 = 0.614$

$(\Sigma x^2)(\Sigma y^2) = 15.353$

$\sqrt{(\Sigma x^2)(\Sigma y^2)} = 3.918$

$\Sigma xy = 1.312$

$\frac{\Sigma xy}{\sqrt{(\Sigma x^2)(\Sigma y^2)}} = 0.33$

$r = 0.33$

$p =$ less than 0.01 (Simpson, Roe, and Lewontin, 1960; p. 426 Table V)

Regression Line (Figure 1).

Columba livia:

1.) Regression Equation From Arkin and Colton (1956).

$$Y = (a)(X)^b \; ; \; \log Y = \log a + b \log X$$

$$\frac{BOC}{Wt.} = (a)(Wt.)^b \; ; \; \log \frac{BOC}{Wt.} = \log a + b \log Wt.$$

2.) $b_y = \frac{\Sigma xy}{\Sigma x^2}$; (Simpson, Roe, and Lewontin, 1960)

$X = \log Wt.$

$Y = \log \frac{BOC}{Wt.}$

$$\Sigma xy = \Sigma XY - \frac{(\Sigma X)(\Sigma Y)}{n} \qquad -\frac{6,779.302}{56} = -121.059$$

$\Sigma X = 115.597$ $\qquad -131.030$

$\Sigma Y = -58.646$ $\qquad -121.059$

$n = 56$ $\qquad -9.971$

$\Sigma XY = -131.030$

$\Sigma xy = -9.971$

$$\Sigma x^2 = \Sigma X^2 - \frac{(\Sigma X)^2}{n} \qquad \frac{13,362.667}{56} = 238.619$$

$(\Sigma X)^2 = 13,362.667$ $\qquad 250.425$

$n = 56$ $\qquad 238.619$

$\Sigma X^2 = 250.425$ $\qquad 11.806$

$\Sigma x^2 = 11.806$

$$b_y = \frac{-9.971}{11.806} = -0.845$$

Regression Line (Figure 1).

Columba livia:

3.) $\Sigma Y = na + b\Sigma X$ $\quad -58.646 = 56a + (-0.845)(115.597)$

-97.679

$\Sigma Y =$	-58.646	97.679
$n =$	56	58.646
$b =$	-0.845	39.033
$\Sigma X =$	$115,597$	$\frac{39.033}{56} = 0.697$
$a =$	0.697	

4.) $\log \frac{BOC}{Wt.} = 0.697 + (-0.845) \log Wt.$

Wt.	log Wt.		log BOC/Wt.
11	1.0414	$0.697 + (-0.845)(1.0414) =$	-0.183
77	1.886	$0.697 + (-0.845)(1.886) =$	-0.897
155	2.190	$0.697 + (-0.845)(2.190) =$	-1.154
464	2.667	$0.697 + (-0.845)(2.667) =$	-1.557

		BOC/Wt.
-0.183	$= 9.817-10$	$= 0.6562$
-0.897	$= 9.103-10$	$= 0.1268$
-1.154	$= 8.846-10$	$= 0.07015$
-1.557	$= 8.443-10$	$= 0.02774$

5.) Plots For Regression line:

BOC/Wt.	Wt.
0.6562	11
0.1268	77
0.07015	155
0.02774	464

6.) Regression Equation For Columba livia:

$$\frac{BOC}{Wt.} = (5)(Wt.)^{-0.85}$$

Regression Line (Figure 2).

Multi-species sample:

1.) Regression Equetion From Arkin and Colton (1956).

$Y = (a)(X)^b$; $\log Y = \log a + b \log X$

$\frac{BOC}{Wt.} = (a)(Wt.)^b$; $\log \frac{BOC}{Wt.} = \log a + b \log Wt.$

2.) $b_y = \frac{\Sigma xy}{\Sigma x^2}$; (Simpson, Roe, and Lewontin, 1960)

$X = \log Wt.$

$Y = \log \frac{BOC}{Wt.}$

$\Sigma xy = \Sigma XY - \frac{(\Sigma X)(\Sigma Y)}{n}$ $\qquad \frac{-7,405.085}{67} = -110.524$

$\Sigma X = 129.455^-$
$\Sigma Y = -57.202$
$n = 67$
$\Sigma XY = -134.512$

-134.512
-110.524
-23.988

$\Sigma xy = -23.988$

$\Sigma x^2 = \Sigma X^2 - \frac{(\Sigma X)^2}{n}$ $\qquad \frac{16,758.597}{67} = 250.128$

$(\Sigma X)^2 = 16,758.597$
$n = 67$
$\Sigma X^2 = 275.133$

275.133
250.128
25.005^-

$\Sigma x^2 = 25.005^-$

$b_y = \frac{-23.988}{25.005^-} = -0.959$

Regression Line (Figure 2).

Multi-species sample:

3.) $\Sigma Y = na + b\Sigma X$ $\quad -57.202 = 67a + (-0.959)(129.455)$

$\Sigma Y = -57.202$ $\quad -124.147$

$n = 67$ $\quad 124.147$

$b = -0.959$ $\quad -57.202$

$\Sigma X = 129.455$ $\quad 66.945$

$a = 0.999$

$$\frac{66.945}{67} = 0.999$$

4.) $\log \frac{BOC}{Wt.} = 0.999 + (-0.959) \log Wt.$

Wt.	log wt.	log BOC/wt.
21	1.322	$0.999 + (-0.959)(1.322) = -0.269$
100	2.000	$0.999 + (-0.959)(2.000) = -0.919$
462	2.665	$0.999 + (-0.959)(2.665) = -1.557$
3,710	3.569	$0.999 + (-0.959)(3.569) = -2.424$

		BOC/Wt.
-0.269	$= 9.731 - 10$	$= 0.5383$
-0.919	$= 9.081 - 10$	$= 0.1206$
-1.557	$= 8.443 - 10$	$= 0.02774$
-2.424	$= 7.576 - 10$	$= 0.003768$

5.) Plots For Regression line:

BOC/Wt.	Wt.
0.5383	21
0.1206	100
0.02774	462
0.003768	3,710

6.) Regression Equation For Multi-species sample:

$$\frac{BOC}{Wt.} = (10)(Wt.)^{-0.96}$$