THE VENTILATION

OF THE

RESPIRATORY TRACT IN BIRDS

BY

ERIK ZEUTHEN
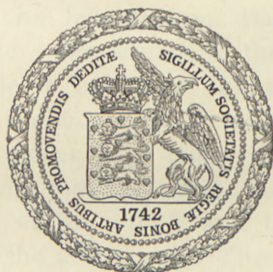
I. EXPERIMENTS ON THE HEN AT REST

A. Earlier investigations on the respiration of birds[1].

a. **Anatomy.** The lung of the bird is a relatively small organ which is confined to the dorsal part of thorax where it is attached to the wall of thorax. The ribs are wedged into the dorsal surface of the lung where they form rather deep furrows. The lungs are ventrally bounded by the pulmonary diaphragm, a formation peculiar to birds. This diaphragm is to be considered as the ventral surface of the lungs themselves. It is a membrane of connective tissue with weak musculature. It arches slightly up into the lungs — hence it must be assumed that the lungs will expand slightly by its contraction. The pulmonary diaphragm is perforated by a number of holes, the ostia. The bronchi of the lung penetrate through these holes and are connected with a number of air sacs which are inserted between the organs of the body cavity. The air sacs frequently also penetrate into the marrow of the bones (being nearly always found, for example, in the humerus and the femur), and they may even extend beneath the skin. Since a diaphragm of the mammalian type is absent, the air sacs lie in one large thoraco-abdominal space. There are 4 air sacs on either side. Named from the front, they are: The interclavicular sac (between the clavicles), the prethoracic sac (level with the lung), the postthoracic sac (at the posterior edge of the lung), and the abdominal sac (filling a large part of the abdomen)[2]. The interclavicular sac is in open connection with the corresponding sac on the other side;

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[1] It is not the intention to give a complete review of the literature. Such a review will be found in WINTERSTEIN (1921) and SCHARNKE (1934).

[2] At the very front we find the unpaired cervical sac, but it is very small and unimportant and will not be taken into consideration here.

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the other sacs are free. While the air sacs in the duck, for example, constitute about 20 % of the body volume, the lungs are small, as mentioned, and tissue + air of the lung represent only 1—2 % of the body volume. In comparison it may be noted that the air of the lungs in man occupies about 5 % of the body volume.
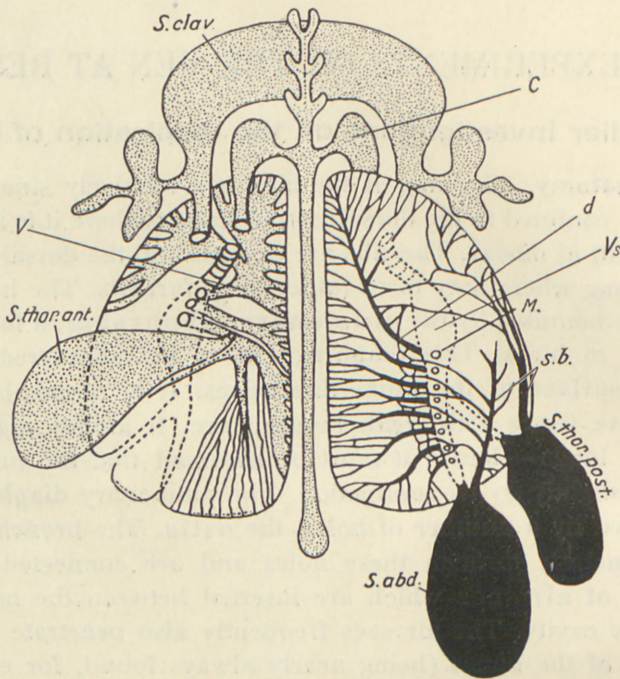

Fig. 1. (From BRANDES)
Lung of a pigeon, seen from the ventral side (left)
and from the dorsal side (right).

C:	Cervical sac	M:	Mesobronchus
S. clav.:	Interclavicular sac	V:	Ventrobronchi
S. thor. ant.:	Prethoracic sac	d:	Dorsobronchi
S. thor. post.:	Postthoracic sac	s. b.:	Saccobronchi
S. abd.:	Abdominal sac	Vs:	Vestibulum

The bronchial system of the lungs is very complicated. Fig. 1 (from BRANDES (1924)) shows, very schematically, the lung of a pigeon, seen from the dorsal side (right) and from the ventral side (left). The trachea and its two branches (the main bronchi) are not shown, but it is seen how the continuation of the main

bronchus, mesobronchus, (*M*) runs through the entire lung, ending, after a single ramification, in the 2 posterior sacs (the abdominal and the postthoracic sac). A number (5—6) of ventrobronchi (*V*) start from the anterior extended part of the mesobronchus, the vestibulum (*Vs*) (fig. 1 left) and branch out on the ventral surface of the lung. 8 to 10 dorsobronchi (*d*) start from the mesobronchus, back of the ventrobronchi (fig. 1 right); their ramifications spread over the dorsal surface of the lung. These two systems of ramified bronchi do not end blindly, but are connected by means of a number of narrow tubes, the air pipes or parabronchi (diameter 0.2—0.5 mm.). The parabronchi run throughout the entire lung tissue in dorso-ventral direction. It should also be mentioned that the two anterior air sacs (the interclavicular and the prethoracic sacs) open into the ventrobronchi.

The above mentioned bronchi have been known for a long time. An entirely new system of bronchi, the saccobronchi, was discovered in 1910 by SCHULZE. The saccobronchi form an extra connection between air sacs and lung. The anterior sacs are in this way connected once more directly with the ventro-bronchi, but the saccobronchi of the posterior sacs (*s. b.* in fig. 1) are connected with a number of longitudinally running para-bronchi in the lateral part of the lung. These parabronchi open towards the front into the ventrobronchi.

The exchange of gases in the lung must be supposed to take place in the air capillaries. These are extremely fine tubes (10—20 μ) which radiate in a very large number from the individual parabronchi. The air capillaries intercommunicate. They are entangled with an equally dense meshwork of blood capillaries, and there is so intimate contact between blood and air capillaries that the question of a common epithelium has been raised.

b. **The mechanics of the respiratory movements and other physiological investigations.** The thorax of birds is very strong. It is cranially and ventrally bounded by the arc consisting of caracoids, clavicles and sternum, on the side by the articulated ribs, and dorsally by the short and rigid vertebral column. In contrast to what is found in man, the respiratory movements in birds are brought about almost exclusively by

means of movements of the ribs. Both inspiration and expiration are active, since we do not find in birds the forces which in man drive the passive expiration, viz., the DONDER pressure and the inspiratory twisting of the costal cartilages. The reason is that costal cartilages are lacking, and the avian lungs are not elastically distended. They may be removed from the body without suffering any essential change of form.

During inspiration, the thorax is expanded in all directions (SOUM (1896), BAER (1896) and ZIMMER (1935)). The ribs move forward and outward, and the arc consisting of caracoids, clavicles, and sternum swings forward and downward with the shoulder as the fixed fulcrum; it follows that the posterior edge of the sternum performs the largest movements during the respiration. Since all the air sacs, as mentioned, are located in one large thoraco-abdominal space, it follows that all sacs, as shown by SOUM, are exposed at the same time to negative pressure and to excess pressure respectively, and hence inspire and expire simultaneously, provided the bronchi leadings to the sacs are open. Vos (1935) tried to form an opinion regarding the participation of the individual air sacs in the ventilation. He let a resting duck inspire pure oxygen, and showed that the increase in the percentage of oxygen was far slower in the anterior than in the posterior sacs. Since moreover the last mentioned sacs are considerably larger than the former, Vos could conclude that the posterior sacs in the duck played a dominating rôle in the respiration at rest. The results of Vos are in harmony with the above mentioned fact, that the amplitude of the respiratory movements is the greatest at the posterior end of sternum.

As mentioned, the lungs are very small in proportion to the sacs, and for this reason alone it does not seem probable that the lungs should be able during inspiration to take up any substantial part of the inspiration volume. That the lungs do expand during inspiration has been shown by SOUM, but the same author also showed that the inspiratory expansion of the lungs was inhibited by the pulmonary diaphragm which contracts during expiration, in direct contrast to the diaphragm in man.

Thus the results of Vos and SOUM point to the air sacs as the parts of the respiratory system which are ventilated by the respiratory volume fluctuations. A question immediately presents

itself. Does a substantial part of the exchange of gases between blood and air take place in the walls of the air sacs? The question must be answered in the negative. The total surface of the air sacs is rather small (of the same of order of magnitude as the surface of the body), and the walls of the air sacs are supplied with blood to an exceedingly slight extent. Moreover, Soum was able to lead pure CO through an abdominal sac, the ostia of which had been blocked, without obtaining any toxic symptoms in his experimental animal (pigeon); the experiment lasted 15 minutes. Thus the whole exchange of gases must take place in the lungs, and, since the lungs do not undergo any essential fluctuations of volume, air must flow through them in one or in both phases of respiration.

The lungs are inserted between the trachea and the air sacs, and the air sacs have therefore always been considered to be the bellows that ventilate the lungs. It has always been a riddle, however, how the air current could ventilate the respiratory parts of the lung when the air sacs are directly connected with the trachea through the largest bronchi of the lung (mesobronchus and ramifications), while the respiratory sections are connected onto this main line through narrow side channels. First Brandes (1924) and then Bethe (1925) thought to solve this problem by assuming the presence of a large number (13—15) of valves or muscular sphincters in each lung. These valves should work in time with the respiration and thus force all the air through the parabronchi — according to the theory of Bethe in such a way that the direction of flow in the parabronchi was the same (dorso-ventral) in both phases of respiration.

The theories of Brandes and Bethe are purely speculative. And the attempts of later authors to substantiate them must be considered to have failed (Dotterweich (1930 1. and 2., 1936), Walter (1936), Scharnke (1934, 1938), Vos (1935)). Thus it has been impossible to demonstrate the presence of valves or sphincters in the lung of the bird. We are therefore still in need of an answer to the question of how the ventilation of the lung is achieved by a flow of air if, as it is generally assumed, the main connection between trachea and air sacs passes by the respiratory parts of the lungs.

B. The author's own investigation.
1. Introduction.

Based on the data of FISCHER (1905) and SCHULZE (1910) the author has been able to draw a highly schematized diagram of the lung of the hen (fig. 2). The 2 anterior air sacs are combined into one, and the same applies to the 2 posterior sacs. The 5 ventrobronchi and the 8 dorsobronchi are represented by one of each. The same applies to the saccobronchi of which each sac actually has several. For the purpose of clearness the drawing shows the medial parabronchial system, the main direction of which is dorso-ventral, turned an angle of 90° so that it is now located in the plane of the paper. FISCHER made a large number of measurements of the diameters of the individual bronchi, and it was possible, on this basis, to calculate the cross sectional areas of the most important bronchi with a fair degree of accuracy. The results are recorded at the extreme right of the figure. The cross section of the mesobronchus has not been measured by FISCHER, but it is narrower than the main bronchus (which has been measured) before its entrance into the lung. The figures show the surprising result that the aggregate cross sectional area of all ventrobronchi as well as all dorsobronchi is definitely larger than the cross sectional area of mesobronchus. Finally, the total cross sectional area of the parabronchi is at least 10 times as large as the cross sectional area of the mesobronchus. The sacco-bronchi were not known to FISCHER, but their total cross sectional area is (according to SCHARNKE (1938)) of about the same magni-tude as the cross sectional area of the mesobronchus.

Until now it has been considered a basic principle of the physiology of the avian lung that the bronchi leading to the respiratory section of the lung should be very narrow in relation to mesobronchus. This idea must be abandoned. Moreover, since there is a distance of about 10 mm. between the points at which a ventrobronchus and its connected dorsobronchus open into the mesobronchus, it follows of necessity that the air which reaches the ventrobronchi from the trachea during the inspiration has two possible paths to follow in its further progress towards the posterior air sacs (these, as it will be shown, being by far the most important of the air sacs), namely, either the short passage

through mesobronchus, or the longer, but wider through ventro-
bronchi, parabronchi and dorsobronchi (or saccobronchi). The

The Lung	Bronchi and air sacs	Number	Aggregate cross section
	Trachea		?
	Main Bronchus		12 mm²
	Anterior air sacs	2	
	Vestibulum	1	?
	Ventrobronchi	5	18—35 mm²
	Parabronchi	1000	130 mm²
	Mesobronchus	1	?
	Dorsobronchi	8	25 mm²
	Saccobronchi	?	?
	Posterior air sacs	2	

Fig. 2. Diagram of the hen's lung.
For explanation see text.

same passages must be considered to be open for the expiratory
air, moving in the opposite direction. The ratio between the
quantities of air which pass either way during the inspiration or
expiration must be determined by the resistance to the air cur-
rent of the passages in question. Nothing definite can be said

regarding the resistance of these passages, but it would seem probable that a not unsubstantial part of the air passing to or from the air sacs must pass through the parabronchi.

The above point of view is supported by the following considerations: Strictly speaking, it is only possible to apply POISSEUILLE's law to the movement of liquids and gases in narrow tubes when it is a question of flow through smooth and straigth tubes, and when the flow is laminar. Although the avian lung does not present a tubular system of this kind, we may nevertheless apply POISSEUILLE's formula to a rough estimate of the quantity of air, Q_M, which must flow through the mesobronchus, in comparison with the quantity of air, Q_p, which passes through the parabronchi at the same time. We shall here completely ignore the dorso- and ventrobronchi and their possible resistances. There remain, then, 2 systems of parallel tubes: About 1000 parabronchi with radius $(r) = 0.2$ mm., and 1 mesobronchus with radius $(R) = 0.8$ —1.5 mm. (estimated). For the sake of simplicity we shall assume that the difference in pressure that drives the air is the same for both tubular systems — the tubes are assumed to be smooth, straight and of equal length, and the flow laminar. The last assumption is supported by rough estimates which show that the velocities of flow in the lung of the bird, even in flight, must lie far below the critical limit at which the flow in smooth tubes becomes turbulent. As far as smoothness is concerned, this is indicated by observations on living pigeons where the parabronchi appear surprisingly smooth.

POISSEUILLE's formula states that the resistance to the flow in a tube is inversely proportional to r^4. In the present case we find $\dfrac{Q_M}{Q_p} = \dfrac{R^4}{r^4 \cdot 1000}$. For $r = 0.2$ and $R = 0.8$, 1.0, 1.2 or 1.5 mm., $\dfrac{Q_M}{Q_p}$ will be 0.25, 0.6, 1.3 and 3.2, respectively.

In a schematic system like the one sketched we must therefore expect a considerable flow of air through both of the parallel tubular systems.

What has been said in this introduction will, in the author's opinion, remove the very foundation for the theory of BRANDES and BETHE.

The purpose of this paper is first of all to ascertain whether the avian lungs are actually ventilated in both inspiration and expiration, and, next, to obtain as far as possible a measure of

the ventilation of the lung in both phases of respiration. The following may be said regarding the principles on which the investigation is based: As already pointed out by Vos (1935) it is only possible to explain the CO_2-content ($> 2 \, ^0/_0$) of the air in the sacs if we assume that part of the inspired air has passed the lung on its way to the sacs. The reason is that the diffusion into the sacs of CO_2 from the walls of the sacs is negligible (Soum) and inspiration into the sacs of the air remaining in the dead space from the preceding expiration can only explain the presence of about $0.5 \, ^0/_0$ CO_2 in the sacs (see also the footnote on p. 25). If we know the percentage of CO_2 in the air that reaches an air sac from the lung (say $6 \, ^0/_0$) as well as the percentage of CO_2 in the air of the sac (say $3 \, ^0/_0$), it is possible to calculate how large a part of the air going to the sac has passed the lungs (in the example given it is $50 \, ^0/_0$). The total respiratory ventilation of the lungs can then be calculated as the sum of the quantities of air that pass the lungs on the way to the individual air sacs.

If the percentage of CO_2 in the expired air is substantially higher than the CO_2-percentage of the air of the sacs, it must mean that during the expiration part of the air must have passed the lungs on its way from the sacs. It is possible to carry out an approximate calculation of the expiratory ventilation of the lungs on the basis of the percentage of CO_2 in the expired air, in the air sacs, and in the air of the lungs. A calculation of this kind, together with the calculation of the inspiratory ventilation of the lungs, will be given later (p. 33—37).

In order to calculate the ventilation of the lungs according to these principles it is necessary to know the ventilation of the individual air sacs. We must calculate the part of the inspiration volume which passes to each individual air sac (p. 13—22). Experiments with inspiration of a foreign gas (H_2) and measurement of the velocity with which it appears in the individual sacs will form the basis for these calculations.

It will be found (p. 22—26) that the previously mentioned calculation of the ventilation of the lungs is only possible after thorough considerations and calculations on the exchange of gases in the avian lung. These considerations will be outlined on p. 27—33.

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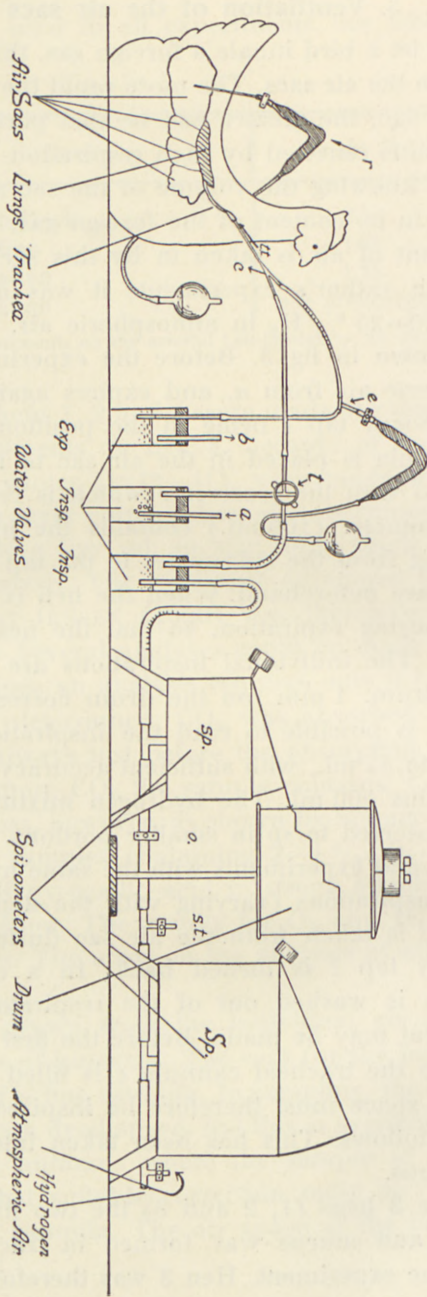Fig. 3. Apparatus for investigating the ventilation of the air sacs.

t. t. Connection of the tracheal cannula with trachea
c.   Ramification of the tracheal cannula
e.   Side tube for sampling of the expiration air
t.   Three-way tap

sp. and Sp. Spirometers with hydrogen mixture
o.   Pinchcock for stopping between the spirometers
s. t. Side tube for sampling of the hydrogen mixture
r.   Receiver for air samples

but the intact trachea was connected directly with the tubing of the apparatus by means of a curved glass tube which was led from the mouth cavity down through the glottis and fitted closely to the walls of trachea. The formation of mucus was insignificant in this hen since the cannula was removed after each experiment. The coughing reflex was partly inhibited by intramuscular injection of 0.4—0.8 mg. of codein. Hens 1 and 2 sat free and quietly on the table, while hen 3 had to be fixed in a suitable manner.

After the experiments the inspiratory volumes of the air sacs were determined as follows: The hen was strangled in the position of inspiration and was then frozen in this position. Openings were now made into the individual air sacs, and the sacs were filled with melted paraffin (Vos' method). The weight of the paraffin blocks after hardening, and the specific gravity of the paraffin, could then be used in calculation of the volumes, taking into account the contraction of the paraffin upon cooling.

At inspiration the air is heated from room temperature to the body temperature of the hen (about $40°$) and is, at the same time, saturated with water vapour at $40°$. Correction has been made in the calculations for the expansion due to the increase in temperature, by figuring in the above volume determinations the volume of the sacs at the temperature of the experiment, not at $40°$. The expansion caused by the higher vapour pressure at body temperature has not been taken into account. The resulting error is insignificant.

As an example of how the volume of air which is taken up by an air sac per inspiration can be calculated from the increase measured in the H_2-percentage of the sac, we shall here give the calculation of the ventilation of the right abdominal sac in hen 3, in the experiment of 25.I.1941 (see table 4). In the inspiratory position the right abdominal sac holds 28 ml. The hen inspired a mixture containing 12.2 $\%$ H_2. After 3 inspirations the air of the sac contained 9.2 $\%$ H_2. Trial and error methods were used in the calculations. First, an attempt was made to find out whether inspiration into this sac of 40 or 50 $\%$ of the total inspiration volume of the hen in the course of 3 inspirations could bring the H_2-percentage of the sac up to the measured H_2-percentage of the inspired hydrogen mixture. It was found that the assumed

40 % led to a too small, and the 50 % to a too large increase in the H_2-content of the sac. By narrowing this down it was found that 47 % of the inspiration volume of the hen was taken up by the air sac investigated. This final calculation is reported below. In this calculation it has been assumed as reasonable that also 47 % of the dead space air (trachea + mesobronchus = 5.4 ml.),

Calculation.

1st. inspiration: 30 ml.

Dead space + air of the lung:

$$\frac{(5.0+5.4)\cdot 47}{100} + 2.2 = 7.1 \text{ ml.}$$

Hydrogen mixture:

$$\frac{30\cdot 47}{100} - 7.1 = \qquad\qquad 7.0 \text{ ml.} \quad H_2\text{-mixture}$$

After 1st. inspiration: 7.0 ml., or 25 % of the volume of the air sac (28 ml.).

Expiration:

$$\frac{14.1\cdot 25}{100} = \qquad\qquad 3.5 \text{ ml.}$$

Residue in sac   3.5 ml. H_2-mixture

2nd. inspiration: 34 ml.

Dead space + air of the lung:

$$\frac{5.4\cdot 47}{100} + 2.2 = 4.7; \quad \frac{4.7\cdot 25}{100} = 1.2 \text{ ml.} \qquad —$$

Hydrogen mixture:

$$\frac{34\cdot 47}{100} - 4.7 = \qquad\qquad 11.3 \text{ ml.} \qquad —$$

After 2nd. inspiration: 16.0 ml., or 57 % of the volume of the air sac.

Expiration:

$$\frac{16.0\cdot 47}{100} = \qquad\qquad 9.2 \text{ ml.}$$

Residue in sac   6.8 ml. H_2-mixture

3rd. inspiration: 34 ml.

Dead space + air of the lung:

$$\frac{5.4\cdot 47}{100} + 2.2 = 4.7; \quad \frac{4.7\cdot 57}{100} = 2.7 \text{ ml.} \qquad —$$

Hydrogen mixture:

$$\frac{34\cdot 47}{100} - 4.7 = \qquad\qquad 11.3 \text{ ml.} \qquad —$$

After 3rd. inspiration: 20.8 ml., or 75 % of the volume of the air sac.

and at the 1st inspiration also 47 °/$_0$ of the air standing in the inspiration tubing from t to c (5 ml.) have been inspired by this sac. In this as in all calculations on the ventilation of the abdominal sacs it has been assumed that 40 °/$_0$ of the air from both lungs pass to each abdominal sac; this corresponds to 2.2 ml. It is moreover assumed that the dead space and the lung before each inspiration contain air of the H_2-percentage which was attained in the sac at the previous inspiration. Finally, it is also assumed that each inspiration is followed by an equally large expiration.

The reliability of this calculation is essentially dependent on the accuracy with which the volumes of the sac and the lung can be determined, and this accuracy is certainly not great. Thus the volume of the lung is simply determined by perfusion of a lung with warm paraffin from the main bronchus, followed by a melting off and weighing of the paraffin. In order to investigate the possible magnitude of the error of calculation, an examination has been made (using the above calculation as example) to determine within what limits the result will vary when we vary the volume of the air sac and the volume of the lung within wide limits. The variations which the author considers possible are shown in braces in table 2. It will be seen from this that the percentage found in the example used may be given as 47 ± 5 °/$_0$.

In the calculation of the ventilation of the small pre- and postthoracic sacs we encounter the great difficulty that the dead space (trachea + large bronchi) as well as the volume of the lung prove to be large in proportion to the quantity of air taken in by these sacs per inspiration (about 20 °/$_0$ of the inspiration volume). In the calculations, which are therefore subject to a large percentage but a small absolute error, it has been assumed that 10—15 °/$_0$ of the air from the dead space and from the lung are inspired by the prethoracic sacs, and 10—5 °/$_0$ by the post-thoracic sacs. The interclavicular sac in the hen is much smaller than in the duck. The author did not succeed in puncturing it, and its ventilation has therefore not been measured. In the calculations based on the experiments by Vos on the duck (to be reported later) it was found that the ventilation of the inter-clavicular sac is almost zero. The same is probably true in case of the hen.

Table 2.

Air sac volume ml.	air space of the lung ml.	Per cent of inspired air passing to the air sac
22.	2.2	40
25	2.2	44
28	2.2	47
31	2.2	52
34	2.2	56
28	0	40
28	1	43
28	2	46
28	3	51
28	4	55

The effect on the calculated result (last column) of (1) varying the volume of the air sac (1st. column) with constant air space of the lung, and (2) varying the air space of the lung (2nd. column) while keeping the air sac volume constant.

Table 3.

The volumes of the different air spaces of the hen's respiratory tract, corrected to the temperature of the experiments (ml.).

Hen No.	Abdominal air sacs	postthor. air sacs	prethor. air sacs	intercl. air sac	Volume of the		Dead space
					whole lung	air space of lung	
1	left 25 right 38	6 ..	12 ..	9	.. 8	.. 3	1.1
2	left 32 right 44	2.1 2.0	9 8	..	.. ..	.. ..	1.0
3	left 18 right 28	2 to 3 3 to 4	5 to 6 7 to 8	9	.. 10	.. 2.5	2.7 [1]) 5.4 [2])

[1]) Without cannula.   [2]) With cannula.

Results: Table 3 records, for the hens employed, the volume determinations of the air sacs, the lungs, and the dead space (mesobronchus and trachea up to the branching out of the tracheal cannula). Table 4 records all experiments and results of calculations dealing with the ventilation of the air sacs. Hen 1 was suffocated by mucus in trachea on the second night after the operation. It probably died in the position of expiration, or

Table 4.

The ventilation of the different air sacs of the hen.

Hen and date	air sac	inspirations		hydrogen in the		a/b	dead space ml.	% of insp. air passing to the air sac
		frequency per min.	depth ml.	air sac a per cent after insp.	insp. air b per cent			
1. 4. XII 1940	right abdom.	16	14.0 15.3 14.7 16.3 16.1 16.4	8.3	14.2	0.58	1.1+5 1.1 1.1 1.1 1.1 1.1	51
1. 4. XII 1940	left abdom.	24	12.3 15.0 12.4 15.7 15.1 13.8	8.3	14.2	0.58	1.1+5 1.1 1.1 1.1 1.1 1.1	46
1. 4. XII 1940	left post-thor.	24	12.8 12.7 13.0 14.2 12 6 14.0	7.2	14.2	0.51	1.1+5 1.1 1.1 1.1 1.1 1.1	6
1. 4. XII 1940	right pre-thor.	18	13.1 13.1 14 4 16.0 14.1 14.8	5.3	14.8	0.36	1.1+5 1.1 1.1 1.1 1.1 1.1	8
2. 18. XII 1940	right abdom.	14	22 8 19.7 28.7 29.0 23.5	9.2	15.6	0.59	1.1+5 1.1 1.1 1.1 1.1	42
2. 18. XII 1940	left abdom.	15	22.9 23.2 26.4 23.7 22.5	10.9	15.6	0.70	1.0+5 1.0 1.0 1.0 1.0	42
2. 18. XII 1940	right post-thor.	21	18.6 17.5 17.3 17.0	7.3	22.0	0.33	1.0+5 1.0 1.0 1.0	1.5

2*

Table 4 (continued).

Hen and date	air sac	inspirations		hydrogen in the		a/b	dead space ml.	% of insp. air passing to the air sac
		frequency per min.	depth ml.	air sac a per cent after insp.	insp. air b per cent			
3. 20. I 1941	left abdom.		37.0 36.0 37.0 34.0	14.6	17.0— 18.0	0.81— 0.86	5.4+5 5.4 5.4 5.4	31— 33
3. 25. I 1941	right abdom.	13	30.0 34.0 34.0	9.2	12.2	0.75	5.4+5 5.4 5.4	47
3. 29. I 1941	left abdom.	15	23.0 20.0 35.0 37.0	19.0	22.8	0.83	5.4+5 5.4 5.4 5.4	34
3. 1. II 1941	right pre-thor.	15	47.0 43.0	2.9	11.8	0.25	5.4+5 5.4	4
3. 4. II 1941	right post-thor.	14	35.0 37.0	4.0	21.4	0.19	5.4+5 5.4	1.5
3. 4. II 1941	right post-thor.	14	36.0 34.0 41.0 32.0	12.6	21.4	0.59	5.4+5 5.4 5.4 5.4	3

The deep inspirations of hen 3 are due to the low temperature (5—10°) of these experiments and the resulting high metabolism. The temperature was about 20° in case of hens 1 and 2.

in the act of expiration. The experiment on this hen is therefore of less value, but it does show the relative ventilation of the individual sacs. It applies to all hens that the increase in H_2-percentage is most rapid in the posterior sacs. The mass of air is here, as in the duck (Vos) renewed more rapidly than in the anterior sacs. The experiments on hens 2 and 3 show that about 80 % (70—90) of the total inspiration volume pass to the abdominal sacs, 8—15 % to the prethoracic sacs, and 3—12 % to the postthoracic sacs. The interclavicular sac presumably takes 0—1 %. Theoretically it should be possible to calculate the inspiratory dilatation of the lungs as the difference between the

total inspiration volume and the sum of the inspiration volumes of the individual sacs, but the figures do not permit a calculation of this kind. Assuming, however, that the percentage expansion of the lungs is of the same magnitude as that of the prethoracic sacs (which lie level with the lungs) we find that the lungs may take up 4 % of the inspiration volume by their increase in volume. Since the pulmonary diaphragm contracts during expiration, it follows that even this figure may be too high.

As a last result we shall emphasize that the percentage participation in the ventilation of the individual sacs is independent of the depth of the inspirations.

4. Ventilation of the air sacs in the duck.

(Calculations based on the experiments by Vos).

As mentioned on page 6 Vos concluded from his oxygen inspiration experiments that the posterior sacs in the duck (the abdominal and postthoracic sacs) play a dominating rôle in the respiration at rest. How dominating a rôle is not apparent until we attempt a calculation of the ventilation of the individual air sacs. Such an attempt is made in table 5. The calculation is

Table 5.

The ventilation of the air sacs of the duck.

air sac	volume determinations ml.	number of experiments	per cent of inspired air passing to the air sac
both abdominal air sacs	65 + 80 = 145	4	49[1])
both postthor. air sacs	27 + 30 = 57	12	23
both prethor. air sacs	11 + 13 = 24	8	3
interclav. air sac	53	11	1
dead space	4		

Total... 76 per cent

[1]) Vos' experiment No. 3 has not been included in these calculations because it differs distinctly from the other experiments on these air sacs.

based on the principles given above for the hen. Vos did not
measure the depth of the individual inspirations, but since he
states that the duck was always at rest before and during the
experiment, it should be justified to accept a single measurement
of the depth of inspiration (35 ml.) as representative of all
inspirations. Nor did Vos attempt to measure the volume of the
lungs. Hence this volume is not taken into account in the cal-
culations, and the systematic error that follows from this makes
the calculated results 10—15 $^0/_0$ too low. It is probably because
of these sources of errors that we can only account (table 5)
for 76 $^0/_0$ of the total inspiration volume. Of these 76 $^0/_0$, the
72 $^0/_0$ pass to the posterior sacs which are thus playing a very
dominating rôle in the respiration at rest. While the postthoracic
sacs were of quite secondary importance in the hen, they are
essential in the duck. A simple explanation is that the sacs are
widely different in size in the two animals (cf. tables 3 and 5).

5. The CO_2-content of the different parts of the respiratory organ.

In continuation of the programme outlined on p. 10—11 we
shall now proceed with the measurement of the CO_2 of the air
sacs, the expired air, and the air of the lungs, all in the hen at rest.

CO_2-content of the air sacs. At the sampling the hen was
partly free and partly connected with the apparatus shown in
fig. 3. All air sacs contained CO_2 — frequently a rather large
amount. Table 6 shows that the posterior sacs have a CO_2-content
which is lower than that of the anterior sacs.

CO_2-content of the expired air (table 6). The hen was
connected with the apparatus in fig. 3. Samples were drawn
during the whole or a major part of an expiration, from the
expiration tube e. An exception were the samples from hen 3
on 20.I.1941; they were taken at the close of an expiration. It
will be seen that the CO_2-percentage of the first mentioned
samples is distinctly lower than that of the latter (20.I.41). This
must, at least partly, be attributed to the fact that they also
contain CO_2-free air from the dead space.

CO_2-content of the air of the lungs. The hen rested free
and quietly on the table. The air of the avian lung cannot be

Table 6.

Carbon dioxide determinations (in per cent) on samples from the air sacs and the expired air. Where also oxygen analyses have been made, the results of these are given in italics below the corresponding carbon dioxide figure.

Hen and date	Abdominal air sacs		Postthoracic air sacs		Prethoracic air sacs		Expired air
	left	right	left	right	left	right	
1. 25. XI. 40	2.1 *18.5*	2.1 *18.3*	..	..	..	..	..
1. 4. XII. 40	3.1	2.6	3.8	..	3.7	..	4.4 5.7 5.8
2. 9. XII. 40	2.0 *19.2*	2.6 *18.4*	4.8 *15.1*	5.8 *14.6*	4.4 *16.7*	5.1 *14.1*	..
2. 18. XII. 40	..	..	..	..	..	..	5.6 *13.3* 5.1 *13.6*
3. 20. I. 41	3.4	..	..	..	..	..	8.1 7.0
3. 22. I. 41	..	..	..	..	..	..	5.9
3. 23. I. 41	..	..	..	..	..	..	5.2
3. 24. I. 41	..	2.7 2.7	..	..	..	..	6.1
3. 28. I. 41	..	..	..	..	..	..	6.6 6.7
3. 29. I. 41	3.4	..	..	..	..	..	..
3. 1. II. 41	..	..	..	..	..	6.4 6.4	..
3. 3. II. 41	..	..	..	..	..	..	5.5
3. 4. II. 41	..	..	6.1 6.6	..	..	..	..
3. 5. II. 41	..	2.9 3.5	..	..	..	..	5.8 6.2 5.9
3. 10. II. 41	..	3.0 3.5	..	..	..	..	..

Table 6 (continued).

Comments:

25. XI: The animal is intact and quiet. Dead space 2.0 ml. Respiration frequency about 20 min.

4. XII: The hen is connected with the apparatus (fig. 3) through a cannula. Dead space 1.1 ml. Frequency about 20 min.

9. XII: The animal is intact and quiet. Dead space 2.0 ml. Frequency about 20 min.

18. XII: Tracheal cannula. Dead space 2.0 ml. Frequency about 20 min.

All experiments on hen 3: Tracheal cannula: Dead space 5.4 ml. Frequency about 12—15 min. All experiments on this hen were carried out at 5—10°. This explains the deep inspirations (30—50 ml.).

All experiments on hen 1 and 2 were carried out at normal temperature (20°). The inspirations of hens 1 and 2 were about 15—20 ml.

20. I: The 2 expiration air samples have been drawn at the end of an expiration. They are accordingly not contaminated with the CO_2-free air of the dead space, and they are not included in the mean value calculated for this hen.

All other expiration samples in hens 1, 2 and 3 were drawn through the whole or most of an expiration.

obtained for analysis, but a priori we may assume that the air which is inspired into the air sacs from the lung, or was intermixed with the expired air, is comparable to the alveolar air in mammals, since it comes rather directly from the respiratory parts of the lung. KROGH (1910) showed that the CO_2-tension of the arterial blood in mammals is identical with that of the alveolar air. It is therefore to be assumed that a determination of the CO_2-tension of the arterial blood of birds should indicate the CO_2-tension of the air of the lung. Evidently a tonometric determination of the CO_2-tension of the arterial blood should be difficult to perform. CAMPBELL (1924) claimed, however, that the CO_2-tensions in tissues and in the alveolar air of mammals are practically identical, even when it is a question of tissues (subcutis) where the O_2-tension is low (3 $\%$). CAMPBELL injected large volumes of air under the skin or into the abdominal cavity in cats and rabbits. The composition of the injected air changed in accordance with the tension of the gases in the tissues investigated. An analysis of the injected air, after equilibrium had been established, gave information regarding the tension of the gases in the tissues.

In birds the marrow in the larger bones usually contain

diverticula from the air sacs. If, for example, the humerus air sac in the hen is not ventilated, its air must be in equilibrium with the CO_2- and O_2-tensions in the surrounding blood and tissue. The following experiment shows clearly that the humerus section is not ventilated: A hen inspired a mixture containing 21.5 % H_2 in 1 minute (22 inspirations). Immediately after, an air sample was taken from the humerus. No trace of H_2 could be found in this sample[1]. Analysis of the humerus air in the hen showed that the composition of this air was very constant, even from animal to animal (table 7). The O_2-content (11—14 %) is far higher than the O_2-tensions normally found in the tissues — so high that we may well maintain that the humerus air must be in diffusion equilibrium with almost pure arterial blood. Thus the CO_2-tension of the humerus air is identical with the CO_2-tension of the arterial blood, and must therefore be assumed to indicate the CO_2-tension of the air of the lung. In the 4 hens investigated this CO_2-tension should then be 6.0, 5.6, 5.8 and 5.4 — mean 5.7 %.

Having now determined the ventilation and CO_2-content of the air sacs, as well as the CO_2-content of the expired air and of the air of the lungs, it seemed reasonable to believe that the road was clear for a calculation of the inspiratory and expiratory ventilation of the lungs according to the principles laid down on p. 11. Tables 6 and 7 show, however, that the expired air frequently contains definitely more CO_2 than the above determined CO_2-percentage of the air of the lungs, particularly so when the expired air is sampled at the close of an expiration. This does not harmonize with the assumption made on p. 24, that the CO_2-content of the air of the lung should be indicated by the CO_2-tension of the arterial blood. The author must here point out that "air of the lung" is understood to mean the air that leaves the parabronchi during the inspiration and expiration. Thus the above mentioned assumption cannot be maintained,

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[1] If the air space of the humerus is cleared entirely of CO_2, it will take 15—20 minutes before the diffusion equilibrium with the surrounding tissue is again established. Now, it is known from BAER (1896) that the air sacs of the bones are the only air sac sections which are well supplied with blood capillaries. But if we assume that the ingoing diffusion of CO_2 from the walls of the other air sacs, for a certain difference in pressure, occurs with the same velocity as in the humerus sac, then we find that the ingoing diffusion from the walls of the sac at the most can explain the presence of 0.1—0.2 % in the sac.

Table 7.

Carbon dioxide determinations (in per cent) on samples
from the humerus air space. Where also oxygen analyses
have been made, the results of these are given in italics
below the corresponding carbon dioxide figure.

Hen 1		Hen 2		Hen 3		Hen 4	
4. XII	6.0	9. XII	5.5	21. I	5.7	4. XI	5.0
1940	*11.2*	1940	*13.0*	1941	6.1	1940	5.3
	6.0		5.5		5.6		5.0
			13.0		6.0		5.2
			6.2[1])		5.7		*12.6*
			11.3		5.9	5. XI	5.6
						1940	*13.9*
						6. XI	5.3
						1940	5.4
							11.7
						8. XI	5.5
						1940	*11.4*
							5.4
							12.1
							6.2
							10.6
							5.4
							12.4
Mean: 6.0 % CO_2		Mean: 5.6 % CO_2		Mean: 5.8 % CO_2		Mean: 5.4 % CO_2	
11.2 % O_2		13.0 % O_2				12.7 % O_2	

[1]) The hen was asleep just before the sample was drawn. In mammals the arterial
carbon dioxide tension is increased somewhat during sleep. Maybe this is the case also
in birds.

but the air which leaves the lungs during expiration
(and probably also during inspiration) must be con-
siderably richer in CO_2 than indicated by the CO_2-
tension of the arterial blood.

There is here a distinct contrast between birds and mammals,
and we are led directly into considerations of the way in which
the exchange of gases must be considered to take place in a
lung like that of the bird where air flows through the lung. The
question will be considered in the following, after which it should
be possible to revert to the main question, viz., the determination
of the inspiratory and expiratory flow of air through the lungs.

6. The exchange of gases when air flows through the avian lung.

It has previously been mentioned that complete equilibrium between the CO_2-tensions of the alveolar air and of the arterialized blood is obtained in the mammalian lung. No alveoli are found in the avian lung, but the exchange of gases must take place in the air capillaries. However, there is no reason to assume that complete equilibrium between the CO_2-tensions of the air of the air capillaries and of the arterialized blood should not occur in the lung of the bird.

As far as the mammalian lung is concerned, it seems quite clear that the alveolar air under normal conditions has the same composition in the different parts of the lung, and in each individual place shows only a very small variation with the respiratory phase. In case of the avian lung, however, it can be established, as it will be mentioned below, that the composition of the air of the air capillaries varies widely from place to place as well as from time to time during the respiratory cycle. The arterial CO_2-tension is therefore only indicative of the average composition of the air of the air capillaries.

We know that the air flows in the parabronchi, but not whether it also flows in the air capillaries. All we know is that the CO_2 which is given off in the air capillaries (or the O_2 that is consumed) must pass the parabronchi. Moreover, that we have the least favourable conditions for the exchange of gases between parabronchi and air capillaries if the air does not flow, so that all exchange must take place by diffusion in the air capillaries. The maximum difference between the average CO_2-tensions of the air of the air capillaries and of the parabronchial air may be calculated when we assume that the exchange of gases occurs by diffusion in the air capillaries. The calculation is based on KROGH's formula (1920).

$$p - p_1 = \frac{S \cdot l}{k_{CO_2} \cdot a} \qquad (1)$$

where

$p - p_1$ = the difference in pressure to be determined (in atm.),

k_{CO_2} = 0.15,

a = the total cross sectional area of the air capillaries in one lung (sq.cm.),

l = the length of the diffusion path (cm.),

S = the amount of CO_2 to diffuse. Since the calculation here is made for a hen at rest and for one lung, it follows that S is equal to one-half of the metabolism of the hen at rest (ml/sec.).

The figures of Fischer (1905) permitted an approximate measurement of the total cross sectional area of the air capillaries (a). It was estimated to be equal to one-half of the total surface of the parabronchi. Since one lung of the hen contains about 1000 parabronchi with an average length of about 8 mm. and a diameter of about 0.4 mm., the area wanted is $1/2 \cdot 2 \cdot \pi \cdot 0.2 \cdot 8 \cdot 1000 = 5000$ sq.mm. $= 50$ sq.cm. The length (l) of the diffusion path was estimated to be $1/4$ of the distance between the individual parabronchi, or 0.025 cm. S was measured as 0.2 ml/sec. Entering these values in (1) we find $p - p_1 = 0.0007$ atm., or 0.07 % of 1 atmosphere. For a hen at rest the difference between the CO_2-percentages of the parabronchial air and the air of the air capillaries is only 0.07 %, i. e., the percentages are, practically speaking, identical. It follows that the arterial CO_2-tension does not only give the average CO_2-tension of the air of the air capillaries, but also the average CO_2-tension of the parabronchial air.

A few additional remarks will deal with the calculations of the diffusion:

1. The results are valid also for O_2 which in air diffuses with about the same velocity as CO_2 ($k_{O_2} = 0.18$).

2. Ventilation of the air capillaries is superfluous in a hen at rest.

3. It is true that the hen is not a flying bird, but the following example illustrates the tendency in the flying bird: Assuming that the metabolism in the flying bird can rise to a maximum of 25 times the metabolism at rest, it follows that $p - p_1 = 25 \cdot 0.7 = 1.75$ % CO_2. This is thus the maximum difference in pressure between the average contents of CO_2 in the air of the air capillaries and of the parabronchial air in the flying bird. The result indicates that ventilation of the air capillaries will possibly be beneficial in the flying bird, though it is hardly a necessity.

It will be shown later (p. 33—37) that the air actually flows through the parabronchi of the bird's lung in both respiratory phases, and that the direction of flow is reversed when the

respiratory phase changes. During inspiration CO_2-free air flows in at the ventrobronchial end of the parabronchi, and the air becomes gradually richer in CO_2 as it passes through the parabronchi. It is exceedingly difficult, however, to say how high
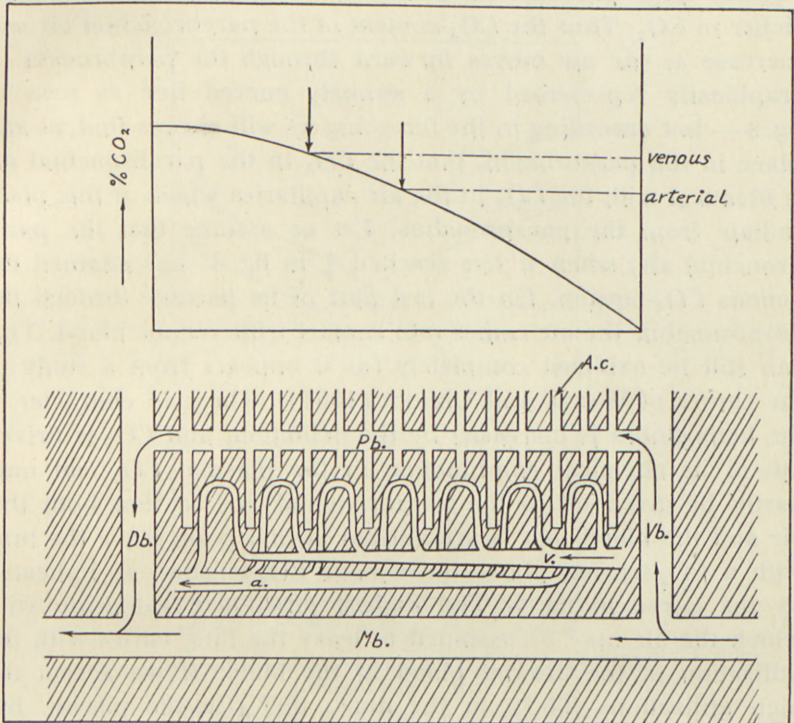

Fig. 4. Below: A parabronchus with blood vessel supply. Above: The CO_2-content of the parabronchial air, arbitrarily drawn.

Mb:	Mesobronchus	$A. c.$:	Air capillaries
Vb:	Ventrobronchus	a:	Arterial blood
Db:	Dorsobronchus	v:	Venous blood
Pb:	Parabronchus (air-pipe)		

The arrows indicate the direction of flow of air during inspiration.

must be the CO_2-percentage of the air that leaves the parabronchi in both respiratory phases. In the parabronchi we have a system of air flow which is shown schematically in fig. 4 (only the inspiratory phase is considered). The air comes into contact with constantly new blood capillaries which all receive venous blood of the same CO_2-tension from the artery of the lung (V). Making

the reasonable assumption that the air, for each millimeter it
moves through the parabronchi, comes into contact with equally
large, but constantly new amounts of blood, it is apparent that
the air will receive constantly smaller amounts of CO_2 from
equally large amounts of blood, since the air itself becomes
richer in CO_2. Thus the CO_2-content of the parabronchial air will
increase as the air moves forward through the parabronchi —
graphically represented by a strongly curved line as seen in
fig. 4 — but according to the foregoing we will always find, at any
place in the parabronchi, that the CO_2 in the parabronchial air
is identical with the CO_2 in the air capillaries which at this place
radiate from the parabronchus. Let us assume that the para-
bronchial air, when it has reached ↓ in fig. 4, has attained the
venous CO_2-tension. On the last part of its passage through the
parabronchus the air comes into contact with venous blood. This
can still be oxidized completely (as it appears from a study of
the curves of WASTL and LEINER (1931)). The acid character of
the hemoglobin is increased by the oxidation, and CO_2 is driven
out of its chemical combination in the plasma. CO_2 can only
partly be given off to the parabronchial air, so that both this
air and the blood that is arterialized at that point leave the lung
with a CO_2-tension above the venous CO_2-tension, as indicated
by the curve in fig. 4. The highest possible CO_2-tension with
which the air may be assumed to leave the lung varies with the
utilization of the arterial blood in the body. If we accept the
high utilizations (60 $^0/_0$ in the duck, 60 $^0/_0$ in the pigeon, but
only 26 $^0/_0$ in the goose!) which have been given by WASTL and
LEINER, we must estimate the highest possible CO_2-tension with
which the air leaves the parabronchi to be 10—11 $^0/_0$. This
tension will (as appears from a study of the curves of WASTL
and LEINER) arise when the venous blood is oxidized in such a
way that no CO_2 can be given off, and hence the CO_2-tension
of the blood is forced up. It should be pointed out that we have
as yet said nothing here regarding the question of whether so
high CO_2-tensions are actually reached in the air that leaves the
parabronchus. Fig. 4 shows that the arterialized blood leaves the
lung with widely different CO_2-tensions, all according to the place
on the parabronchus where it is oxidized.

The foregoing considerations are of importance if we are now

to attempt more accurately to draw the curves for the CO_2-content of the parabronchial air during inspiration and expiration. Moreover, the curves shall be drawn so that the areas above and below the 5.7 $^0/_0$-level (the average tension) are of about the same size. The 2 fully drawn curves in fig. 5 are traced under
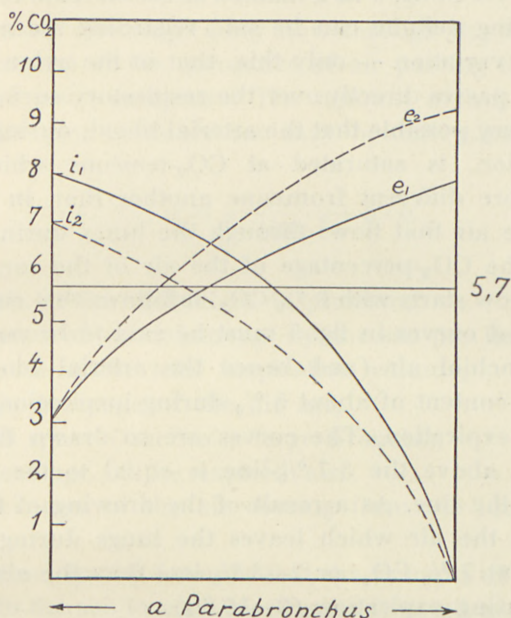

Fig. 5. Hypothetical curves for the CO_2-content of the parabronchial air.
→ Direction of expiratory flow (e_1, e_2)
← Direction of inspiratory flow (i_1, i_2)

the assumption that the composition of the air that leaves the lungs during inspiration and expiration is about the same. At the same time, the areas which are cut off by each curve above and below the 5.7 $^0/_0$-line are about the same, i. e., the CO_2-tensions of the parabronchial air (and hence of the mixed arterial blood) is about 5.7 $^0/_0$ during the inspiration as well as during the expiration. Drawing the curves according to the principles outlined here, we obtain the result that the air that leaves the lungs during inspiration and expiration must contain 7—9 $^0/_0$ CO_2.

In man, however, the composition of the alveolar air (and hence of the arterial blood) varies with the respiratory phases,

so that the alveolar air contains about 0.2 % more CO_2 at the
end of an expiration than at the end of an inspiration. In case
of the hen, the author has actually only determined the average
arterial CO_2-tension to be 5.7 %. If we assume that the arterial
CO_2-tension varies with the respiratory phases it is necessary to
draw the curves in fig. 5 in a manner different from that described
above. Nothing definite can be said regarding the magnitude of
the possible variation — only this, that in the avian lung where
the fresh air passes directly over the respiratory surfaces we must
consider it very possible that the arterial blood, during inspiration
and expiration, is saturated at CO_2-tensions which may be
distinctly more different from one another than in man. Since
moreover the air that flows through the lungs during expiration
starts with the CO_2-percentage of the air of the sacs, while the
inspiratory flow starts with 0 % CO_2, it follows that curves shaped
like the dotted curves in fig. 5 must be said to be possible. Here
the parabronchial air (and hence the arterial blood) has an
average CO_2-content of about 5 % during inspiration, and about
7 % during expiration. The curves are so drawn that the sum
of the areas above the 5.7 %-line is equal to the sum of the
areas below the line. As a result of the drawing of these curves
we find that the air which leaves the lungs during inspiration
contains about 7 % CO_2, or 2—3 % less than the air that leaves
the lungs during expiration (9—10 %).

It is the author's opinion that the 2 types of curves mentioned
represent the possible extremes. Which of the 2 possibilities (or
which intermediate) should be chosen cannot be decided at present.

The curves in fig. 5 show that the CO_2-content anywhere in the
parabronchi, but particularly at their ends, varies with the respiratory
phases. In the bird at rest, however, we still find, anywhere in the
parabronchi, that the CO_2-percentages of the parabronchial air are
identical with those of the air of the air capillaries. It is namely pos-
sible to calculate that, following a fall of 5 % in the CO_2-content of the
parabronchial air, equilibrium between the parabronchial air and the
air of the air capillaries will be reestablished in about $1/50$ second. The
respiratory phases in the hen at rest change each 1 to 2 seconds. It must
be emphasized that in the flying bird, where the respiration frequency
is greatly increased[1] and where the metabolism is multiplied, the fluctu-

[1] According to ZIMMER (1935) and others the respiration during flight is
synchronous with the wing beats.

ations in the composition of the air of the air capillaries will be notice-
ably damped in relation to the fluctuations in the composition of the
parabronchial air.

7. The inspiratory and expiratory flow of air through the lungs.

Inspiration: The inspiratory flow through the lungs is cal-
culated as the sum of the quantities of air passing the lungs on
its way to the individual sacs. The amount of air, x, passing
the lung on its way to an air sac may be determined from the
formula

$$i \cdot \frac{n}{100} \cdot a = s \cdot \frac{n}{100} \cdot e + b \cdot x$$

where

i = the depth of the individual inspiration,

n = the amount of air taken up by the sac per inspiration —
in per cent of the total inspiration volume,

a = the CO_2-percentage of the air sac,

s = the dead space (trachea + large bronchi),

e = CO_2-percentage of the expired air,

b = CO_2-percentage of the air coming from the lung.

It is expressed in the formula that the amount of CO_2 which
is inspired into the sac in each inspiration is equal to the amount
that has its origin in the dead space (which at that time contains
expiratory air) plus the amount that has its origin in the lung.
Since the air that is already contained in the sac (the residual air)
has the same composition as the air mixture which the sac
receives by each inspiration, it is possible to ignore the residual
air in this formula.

Expiration: The expired air is a mixture of the quantities
of air that are expelled from the dead space and from the air
sacs. Knowing the CO_2-content of the individual air sacs, and
knowing how large a percentage each sac contributes to the
expired air, it is possible to calculate the CO_2-percentage, α,
which should be expected if all the sacs expired directly through
the mesobronchus. α lies at 3—4 $^0/_0$ and is thus considerably
lower than the CO_2-percentage actually found in the expired air
(6 $^0/_0$). This means that part of the air expired from the sacs

must have passed the lungs, and the amount, y, may be cal-
culated from the equation:

$$i \cdot e = (i - (s + y)) \cdot a + b \cdot y,$$

where the symbols have the same meaning as in the foregoing
equation. The formula states that the amount of CO_2 in the
expired air must be attributed to CO_2 from the air sacs as well
as CO_2 from the lungs, while the air from the dead space was
free from CO_2.

Results: Since the exact composition of the air that leaves
the lungs is unknown it will now be attempted to calculate the
inspiratory and expiratory flow of air through the lungs on the
basis of the different assumptions that the air leaving the lungs
in both respiratory phases contains 7, 8, 9 or 10 $^0/_0$ CO_2.

Table 8.

Flow of air through the lungs of the hen during inspiration
and during expiration.

	CO_2-percentage of the air that leaves the lungs in inspiration and expiration	Inspiration. Flow through the lungs in $^0/_0$ of inspiration volume	Expiration. Flow through the lungs in $^0/_0$ of expiration volume
Hen 1 + 2	7	14 + 24 = 38	64
	8	11 + 21 = 32	52
	9	10 + 19 = 29	44
	10	9 + 17 = 26	38
Hen 3	7	16 + 25 = 41	87
	8	14 + 22 = 36	67
	9	12 + 19 = 31	54
	10	12 + 19 = 31	46

Hen 1 + 2: $i = 20$ ml. $s = 1.0$ ml. $\alpha = 2.8$ $^0/_0$. CO_2 of the abdominal
sacs = 2.4 $^0/_0$. CO_2 of the thoracic sacs = 4.6 $^0/_0$. CO_2 of the
expired air = 5.5 $^0/_0$.

Hen 3: $i = 35$ ml. $s = 5.4$ ml. $\alpha = 3.8$ $^0/_0$. CO_2 of the abdominal
sacs = 3.1 $^0/_0$. CO_2 of the thoracic sacs = 6.4 $^0/_0$. CO_2 of the
expired air = 6.0 $^0/_0$.

Table 8, 3rd column, gives the quantity of air which passes
the lungs during inspiration, recorded as the sum of the quantity

of air that passes the lungs on its way to the 4 thoracic sacs (the 1st figure, calculated as average CO_2 for these 4 sacs together), and of the quantity of air that passes the lungs on its way to the 2 abdominal sacs (the 2nd figure, determined analogously). All figures are expressed as percentages of the total inspiration volume of the hen. The quantity of air that flows through the lungs during expiration (4th column) is stated directly in percentage of the expiration volume. Because of insufficient analytical results, one calculation is based on the average figures for the CO_2-percentages (table 6) in hens 1 and 2 (hen 1 + 2 in table 8). The average values for hen 3 permitted a special calculation for this hen.

Discussion: The main result, as clearly seen in table 8, is that the lungs are ventilated quite considerably during both inspiration and expiration, regardless of where within the limits of 7—10 $^0/_0$ we estimate the CO_2-content of the air that leaves the lungs during inspiration and expiration. It is not possible at present to establish the absolute magnitude of the ventilation of the lungs, since we (as frequently mentioned) do not know the exact composition of the air that leaves the lungs during inspiration and expiration. For that reason the author must in the following (a and b) confine himself to a discussion of the possibilities at hand.

a) If we assume, in accordance with what was said on p. 31 that the air leaving the lungs during inspiration and expiration contains the same (i. e., 7, 8 or 9 $^0/_0$) CO_2, it will be seen from table 8 that the expiratory flow through the lungs must be about twice as large as the inspiratory flow. With for example 8 $^0/_0$ CO_2 in the air that comes from the lung, we find in hen 3 that 36 $^0/_0$ of the inspiration volume, but 67 $^0/_0$ of the expiration volume must have passed through the lungs. It might be difficult to understand a result like that, from an anatomical point of view, since it would be expected beforehand that the ventilation of the lungs was of about the same magnitude during inspiration and expiration.

It is to be pointed out, however, that the bronchial system of the avian lung is not to be regarded as an entirely rigid tubular system. The lungs expand very slightly during the inspiration, so that the caliber of the individual bronchi in the lung is

increased. Soum has actually observed such a faint inspiratory distension of dorso- and ventrobronchi. If the expansion of the mesobronchus during the inspiration is greater than that of dorso-, ventro- and parabronchi, it should explain why a greater part of the inspiratory, but only a smaller part of the expiratory flow will pass to and from the air sacs by the direct route through the mesobronchus.
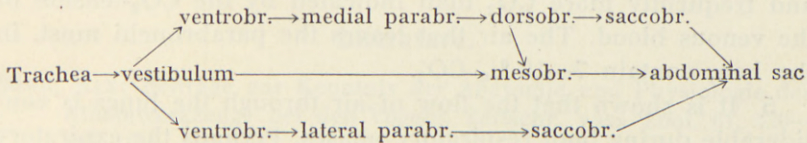
We shall finally mention that, besides the above mentioned passive changes in the calibre of the bronchi of the lung, it is possible that there occur also active changes of the calibre, conditioned upon rhytmical contractions of the musculature of the bronchi. Such active changes of calibre are known from the mammalian bronchioles, the musculature of which is contracted during expiration, and thus narrows the bronchioles — without in any way blocking them, however. The parabronchi of the avian lung are equipped with muscles that strongly resemble the musculature of the mammalian bronchioles. If the ventilation of the avian lung in reality is smaller during inspiration than during expiration, it would be possible to find the explanation in an active inspiratory contraction of the parabronchi. The author does not consider this last theory probable, however, and it is strongly emphasized that it can never be a question of blocking of any bronchial system, but only of a faint — very faint — contraction during one or the other respiratory phase, since it has in fact been demonstrated physiologically that the passage through the parabronchi as well as the passage through the mesobronchus is open in both respiratory phases. Hence we must take exception to any actual valve theory.

b) If we assume, as on p. 32, that the air which leaves the lungs during expiration contains 8—10 $^0/_0$ CO_2, or 2—3 $^0/_0$ more than the air that leaves the lungs during inspiration, we find that the inspiratory flow of air through the lungs is about the same as the expiratory. If for example the air that leaves the lungs during inspiration contains 7 $^0/_0$ CO_2 and the air that leaves the lungs during expiration contains 10 $^0/_0$ CO_2, we find in hen 3 that 41 $^0/_0$ of the inspiratory and 46 $^0/_0$ of the expiratory flow must have passed through the lungs. This result must be said to be in beautiful harmony with the anatomical facts known to date. But as mentioned, it is not possible at present to decide

which one of the two possibilities discussed under a) and b) (or which intermediate) should be given preference.

The following schedule may be drawn for the flow in the bronchi of the avian lung, based on the calculated results. (For the sake of perspicuity only the abdominal sacs are taken into consideration).

Inspiration (cf. diagram in fig. 2).

```
              ventrobr.→medial parabr.→dorsobr.→saccobr.
            ↗                              ↘        ↘
Trachea→vestibulum ────────────────→ mesobr.────→abdominal sac
            ↘                              ↗
              ventrobr.→lateral parabr.────→saccobr.
```

Expiration: All directions of flow are reversed. Perhaps, for unknown reasons, considerably less air is now passing through the mesobronchus.

8. Summary.

1. The passage through the parabronchi in birds is in parallel as regards the flow of air with the direct connection (mesobronchus) between the trachea and air sacs. The parabronchi represent a larger aggregate cross sectional area than the mesobronchus. It follows that part of the air that passes to or from the air sacs must pass the respiratory sections of the lungs, without it being necessary to assume the presence of any guiding valves (as assumed by Brandes and Bethe).

2. In the hen, 80 (70—90) $\%$ of the inspiration volume pass on to the abdominal sacs, 3—12 $\%$ to the postthoracic sacs, 8—15 $\%$ to the prethoracic sacs, and probably 0—1 $\%$ to the interclavicular sac. In the duck (calculations based on experiments by Vos) the corresponding figures were 49, 23, 3 and 1 $\%$ respectively. In the duck it was only possible to account for 76 $\%$ of the total inspiration volume. This is due to experimental errors. The inspiratory expansion of the lungs is slight. In the hen, the lungs can only take up 4 $\%$ (as a maximum) of the inspiration volume and are therefore ventilated almost exclusively by the flowing through of air.

3. It is shown by calculation that the average CO_2-tensions of the parabronchial air and of the air of the air capillaries

must be identical in the bird at rest, and equal to 5.7 $\%$. Both CO_2-tensions vary, however, (parallel) from place to place in the lung, and also, at each individual point, with the respiratory phases.

4. The air flows through the parabronchi and, when leaving these during inspiration and expiration, it always contains more CO_2 than indicated by the tension of this gas in the arterial blood, and frequently more CO_2 than indicated by the CO_2-tension of the venous blood. The air that leaves the parabronchi must, in the hen, contain 7—10 $\%$ CO_2.

5. It is shown that the flow of air through the lungs is considerable during both respiratory phases. Perhaps the expiratory flow is stronger than the inspiratory. In that case it is probable that about 35 $\%$ of the inspiration volume and about 65 $\%$ of the expiration volume have flown through the parabronchi, while the remainder has passed to an from the air sacs through the mesobronchus. It is just as possible, however, that the inspiratory flow through the lungs is about the same as the expiratory. In that case 40—50 $\%$ of both the inspiration and expiration volumes must have passed through the parabronchi. At present, no choice can be made between the two possibilities.

6. A diagrammatic representation is given for the probable directions of flow in the bronchi of the avian lung. All directions are reversed when the respiratory phase changes.

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II. RESPIRATION AND HEAT REGULATION
IN THE BIRD AT REST AT HIGH TEMPERATURE
AND IN THE FLYING BIRD

As already suggested by Soum (1896) and Victorow (1909) the respiratory tract of birds has two functions: that of respiration and that of heat regulation. Most often the needs of heat regulation and of respiration vary independently. Since, however, the loss of heat from the body surface of birds (birds possess no sweat glands) must be assumed to be relatively low and only slightly variable, we must suppose the respiratory tract of birds (which perform a very intense work during flight) to be exceedingly well suited for serving at the same time as a tool of respiration and of heat regulation.

In the hen at rest at low temperature, the loss of heat through the respiratory tract must be assumed to be at a minimum. Accordingly, the ventilated air must be supposed to be utilized as well as possible in respiration. How this is accomplished has been outlined in the preceding paper.

In the hen at rest at high temperature we may expect only a relatively small part of the inspired air to ventilate the lungs, whereas much air must be assumed to ventilate non-respiratory parts of the respiratory tract. In this paper this point will be discussed more in detail.

In the bird, flying at a high rate, finally, we may a priori expect all parts of the respiratory tract to be ventilated at a maximum. However, it will be shown that in flying birds the needs of heat regulation are greatly in excess of the needs of respiration and the consequences of this fact will be discussed.

Since any organ must be constructed so as to comply with the demands of a maximum effort, the anatomy of the avian respiratory tract can only be understood if we consider respiration as well as heat regulation during flight of high intensity. Therefore one of the objects of this paper dealing with respiration and heat regulation during flight is to explain why the lungs of birds have developed into such curious organs.

This paper is almost purely speculative, and I am well aware that many points which I deal with are still open to discussion.

1. The ventilation of the respiratory tract in birds at rest at high temperature.

In a bird at rest at low temperature (say, $< 25°$), the loss of heat from the body surface by radiation and conduction is so high that we may expect the loss of heat by evaporation from the respiratory tract to be at a minimum. In fact, in the preceding paper it has been shown that about 75 % of the air either in leaving or in entering the air sacs under these circumstances flows through the lungs. At low temperature, therefore, the air sacs of birds serve only respiratory purposes.

In hot weather, however, birds largely increase the loss of heat by increasing the ventilation of the respiratory tract (v. SAALFELD 1936). In hot weather respiration becomes very frequent but more superficial than at normal temperature. This type of respiration is named "Hackeln". In the hen the arterial carbon dioxide tension does not measurably decrease during "Hackeln" as will appear from the following: In the preceding paper the arterial carbon dioxide tension of the hen was determined. In 4 hens, resting at room temperature (about 20°), this figure averaged 5.7 %. In hen 2 three determinations (5.5, 5.5 and 6.2) averaged also 5.7. In the experiments to be described here hen 2 was transferred to a hot chamber (30°), where it was placed on a hot radiator. "Hackeln" soon began. The hen respired 200—300 times per minute. After prolonged "Hackeln" a sample was drawn from the humerus air space. Two experiments were performed. In the first experiment ($^{12}/_{12}$ 1940) the sample contained 5.3 % CO_2 and 13.5 % O_2, in the second ($^{13}/_{12}$ 1940) 5.6 % CO_2 and 14.0 % O_2. Since, accordingly, in the hen the

arterial carbon dioxide tension does not decrease at high temperature, the ventilation of the lungs themselves is not increased during "Hackeln". Therefore the increase in ventilation must be localized to the dead space and perhaps also to the air sacs. If the ventilation of the air sacs is increased while the ventilation of the lungs remains unaltered — and the theory is supported by the statement of SCHARNKE (1938), that at high temperature when the pigeon respires very frequently, the carbon dioxide per cent of all air sacs of this bird is lower than at normal temperature — the question arises: can the bird regulate the ventilation of the lungs and of the air sacs independently?

From the diagram fig. 2 in the preceding paper it appears, that if the resistance to the air flowing through the lungs could be augmented, the ventilation of the air sacs might be increased relative to the ventilation of the lungs. In this respect the demonstration of FISCHER (1905) quoted also by BRANDES (1924) of the parabronchial muscles of the avian lung is of interest. These plain muscles do not form a uniform layer, but they lie as a coarse network in the parabronchial wall. Just distal to the muscular network lies a distinct and corresponding network of elastic tissue. When the parabronchial muscles contract, they must therefore be assumed to rise a close system of slimy walls, made up of elastic tissue. Do these muscles represent a variable resistance to the air flowing through the avian lungs?

In order to study this point, I operated from the dorsal side into the lung of a pigeon in ether or amytal narcosis. This can be done, because the avian lung is not kept expanded by a Donder's pressure as is the mammalian lung. When, however, the bird was heated and the respiration became frequent (about 300/min.), no contraction of the parabronchial muscles could be observed (2 experiments were carried out), and this was the case also in a pigeon in which the abdominal air sacs were opened and which was brought into apnoea by sucking large quantities of air through the respiratory tract in the antero-posterial direction, in spite of the fact that the lungs were so greatly overventilated, that the bird remained in apnoea for half a minute after the air current had been stopped. In my opinion, however, in experiments of the above type (narcosis, operation) only positive results may be accepted as convincing, and I therefore

still think it possible, that under physiological conditions the parabronchial muscles may act as variable resistances to the air flowing through the lungs.

That the parabronchial muscles c a n bring about an increased resistance to the air currents in the parabronchi is evident from the following observation: In a pigeon at rest the wall of the para-bronchus is quite smooth, but when stimulated with a hair,
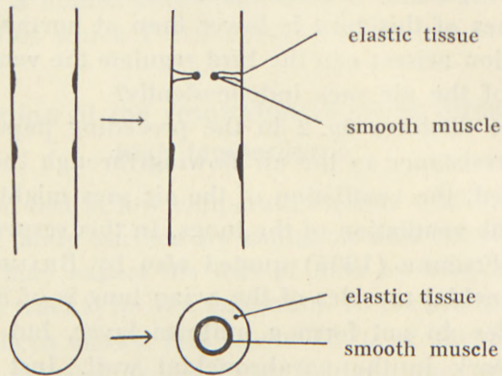

Fig. 1. The parabronchial muscle.
Left: before stimulation.
Right: after stimulation with a hair.

the parabronchial muscles contract after a latency of one or two seconds, and now a slimy wall almost occludes the parabronchus at the stimulated place (fig. 1). This has been observed in both pigeons investigated.

2. The ventilation of the air sacs and of the lungs in birds flying at a high rate.

The metabolism of flight has never been measured, but it is no doubt very high. By calculation carried out in cooperation with the air craft engineer K. G. Zeuthen the metabolism of a pigeon weighing 290 gr. and flying at different velocities was found to be of the order indicated in the table 1, column c (the figures are accurate only to ± 50 per cent). In the calculations, the efficiency of the metabolism of flight has been estimated at 25 per cent. From the table it appears that in the pigeon flying

at the speed of 70 km. per hour (modern measurements indicate the maximum speed of flight in pigeons to be of about 70 to 80 km. per hour), the metabolism is about 27 times the metabolism of rest (the figure of KROGH (1904) for the metabolism of resting pigeons has been made use of). Since in the resting bird at room temperature the expired air contains 5 to 6 per cent carbon dioxide and is saturated with water vapour at about 40°, only 20 per cent (at most) of the heat produced in the metabolism at rest is eliminated by evaporation from the respiratory tract, whereas 80 per cent is lost by convection and radiation from the body surface. Now I do not think it possible for the flying bird to increase the loss of heat from the body surface beyond a certain limit which I estimate to be, say 5 times the loss of heat by the same route in the resting bird[1]. If this is so, an amount of heat equivalent to $0.8 \cdot 5 = 4$ times the metabolism of rest at room temperature represents the maximum of heat which can be eliminated by convection and radiation from the body surface of the bird flying at a high rate at room temperature. But since in the bird flying 70 km. per hour the heat to be eliminated must be of the order $27 \cdot {}^3/_4 = 20$ times[2] the metabolism at rest, this means that an amount of heat equivalent to $20 - 4 = 16$ times the metabolism at rest must be eliminated by evaporation from the respiratory tract. Accordingly, the flying bird must ventilate $5 \cdot 16 = 80$ times as much air as when resting, in spite of the fact that in this example the metabolism is only 27 times the metabolism of rest (more detailed information is given in table 1). In the bird flying at a high rate, therefore, the ventilation of the respiratory tract is about 3 times as high as might be expected when considering the needs of respiration only, and the ventilation of the respiratory tract as a whole must therefore be adjusted in accordance with the needs of heat regulation. These needs are so high, that the ventilation of the lungs should be highly in excess of the needs of the respiration, if the ventilation of the

[1] In duck I observed the bill and the legs to be very warm at high air temperature. KALLIR (1931), however, found the temperature of a bird's skin always to be high and not to be lowered, when an air current was directed against the bird from in front.

[2] Since the efficiency of the metabolism of flight has been estimated at 25 per cent, 25 per cent of the energy evolved during flight is transformed into work and thereupon into heat of friction.

Table 1.

a	b	c	d	e	f	g	h	i
Speed km/ hour	Energy to overcome the resistance Cal/hour	Metabolism Cal/hour	Metabolism of flight × metabolism of rest	Heat to be eliminated Cal/hour	Loss of heat by radiation and conduction Cal/hour	Loss of heat from the respiratory tract Cal/hour	Ventilation during flight × ventilation during rest	$\dfrac{h}{d}$
0	0	2.3	1	2.3	1.8	0.5	1	1
30	1.2	7.1	3.2	5.9	?	?	?	?
40	2.8	13.5	5.9	10.7	?	?	?	?
50	5.4	23.9	10.4	18.5	9	9.5	19	2.0
60	9.3	39.5	17.2	30.2	9	21.2	42	2.4
70	17.8	61.5	26.8	46.7	9	37.7	76	2.8

respiratory tract was accomplished just as in the bird at rest at low temperature. In all probability, however, the air does not pass to and from the air sacs of the flying bird just as in the bird at rest at low temperature. In fact, the few indications available go to show, that during flight the ventilation of the air sacs is increased relative to the ventilation of the lungs. According to SCHARNKE (1938), for instance, the carbon dioxide per cent of all air sacs is lower in a flapping pigeon than in a pigeon at rest at room temperature and whereas Vos (1935) showed the interclavicular air sac of the duck at rest not to be ventilated at all, SOUM (1896) and SCHARNKE (1938) made it probable, that in the flying pigeon this air sac is intensely ventilated. If the ventilation of the air sacs is increased relative to the ventilation of the lungs of the flying bird, the question (already dealt with when discussing the ventilation of the bird at rest at high temperature) at once arises: do the lungs possess variable resistances? And, if we accept the parabronchial muscles as variable resistances: do they contract during flight? This question can not be settled at present, and here I only refer to the statements on p. 44 of the present paper.

The expired air and the arterial carbon dioxide tension in the flying bird. In the hen at rest, the expired air contains about 6 per cent carbon dioxide. When accepting the above

view point that in the intensely flying bird the ventilation of the respiratory tract is about thrice the ventilation to be expected from the needs of respiration only, this involves the statement that in intensely flying birds the expired air contains only $^6/_3 = 2$ per cent carbon dioxide, and if, moreover, the air runs through the lungs just as in the hen at rest at low temperature, the arterial carbon dioxide tension should be $5.7/3 = 1.9$ per cent or, as a maximum, $1.9 + 1.7 = 3.6$ per cent carbon dioxide (1.7 per cent is the pressure difference necessary to transport by diffusion in the air capillaries the gases involved in metabolism of intense flight). As outlined above, however, during flight the ventilation of the air sacs is most probably increased relative to the ventilation of the lungs. If this is so, the arterial carbon dioxide tension is not so low as calculated above.

Flight at great heights. Many birds are known to fly at great heights. Whereas some of these birds, such as the eagle, (7000 m.), glide in the air without moving the wings, others perform an intense work at great heights, as they move the wings constantly during flight. As an example of this last type I quote *Anas crecca* which has been observed in the Himalayas 5600 m. above the sea (GROEBBELS, p. 181). When this bird in flight of constant and high intensity ascends from 0 m. to 5600 m. it can not (even at constant temperature) — as mammals do — increase the ventilation of the respiratory tract, since to fulfill the thermoregulatory needs, the ventilation of the respiratory tract must remain constant at all heights. If, however, the lungs of the flying bird is (or can be) highly overventilated in all heights, it is much easier to understand how birds can perform such hard work at great heights. In an overventilated lung, the blood is coming into contact with air of low carbon dioxide content and relatively rich in oxygen. Both circumstances improve the binding of oxygen by the hemoglobin (the oxygen dissociation curve of the avian blood resembles that of human blood, except that it is a little less steep (WASTL and LEINER (1931), CHRISTENSEN and DILL (1935)).

The capacity of the air sacs as heat regulating organs. From the work of ZIMMER (1935) and others it seems probable that during flight the respiratory movements are synchronous with the wing beats, which MAREY (1890) in flying pigeons deter-

mined at 8/sec. VICTOROW (1909) and ROCHÉ (1891) determined
the volume of all air sacs in the pigeon at 70 and 74 cc., re-
spectively. In pigeons flying 70 km/hour I calculated the ven-
tilation necessary to eliminate all the heat formed in metabolism
to be so high that about 50 cc. must be ventilated per respiration.
Since 50 cc. must be very near the maximum quantity of air
which can be inspired per inspiration by a pigeon, I believe
70 km. per hour to be the maximum speed of flight in pigeons
(when critically considering all errors in the calculations the
figure may be given as 70 ± 10 km. per hour). Of course other
processes may be limiting factors even before this speed has
been attained (circulation, capacity of the muscular machine).
However, modern measurements of the speed of flight in birds
seem to agree well with the above figure.

In my opinion, the above considerations give a clear under-
standing of the strange anatomy of the avian respiratory tract:
The lungs and the air sacs are organs of respiration and of heat
regulation, respectively. The air sacs, however, function only as
heat regulating organs in the flying bird (and perhaps also in
the bird at rest at high temperature), and even during flight as
well as during rest the air sacs serve also respiratory purposes,
since they ventilate the lungs in both respiratory phases. During
flight, the ventilation of the air sacs is most probably in excess
of the ventilation of the lungs, and only a minor part of the air
entering or leaving the air sacs flows through the lungs. This is
why the air sacs directly communicate with the trachea through
the wide mesobronchus and why the lungs communicate with
the mesobronchus much in the same way as a radiator is con-
nected with the pipe carrying the hot water. Just as the quantity
of water which flows through the radiator may be adjusted
independently of the flow through the main pipe by simply
turning the cock, I advance the theory that the ventilation of
the lungs may be regulated independently of the ventilation of
the air sac by means of variable resistances in the lungs. Perhaps
the parabronchial muscles act as such variable resistances. If
this is so, we may assume the parabronchial muscles in the bird
at rest at low temperature to be relaxed (and in fact they have

been observed to be so) whereas they must be assumed to contract to some extent in birds flying at a high rate in the lowlands, but again to relax during flight in great heights.

Summary.[1]

1. In the hen at rest at high temperature the ventilation of the lungs remains unaltered as compared with the ventilation of the lungs at low temperature. But the ventilation of the dead space, and in the pigeon most probably also the ventilation of the air sacs, is increased as compared with the ventilation at low temperature. If, in hot weather, the ventilation of the air sacs is increased relative to the ventilation of the lungs, this might be explained by assuming the resistance to the air flowing through the lungs on its way to and from the air sacs to be increased. The possibility of the parabronchial muscles to act as variable resistances is suggested, but direct experimentation, which cannot, however, be considered convincing, failed to demonstrate this. When stimulated mechanically, the parabronchial muscles contract, almost to the point of occluding the parabronchus.

2. In the flying bird, the thermoregulatory needs may become so high that the ventilation of the respiratory tract may be about 3 times as high as to be expected when considering the needs of respiration only. If, therefore, in the flying bird, the air passes to and from the air sacs just as in the hen at rest at low temperature, the arterial carbon dioxide tension should be as low as 1.9 to 3.6 per cent as compared with the tension 5.7 per cent in the hen at rest. However, in the bird flying at a high rate, I assume the parabronchial muscles to be suitably contracted so as to avoid an overventilation of the lungs. Only in the bird flying at great heights, I do not think that these muscles contract.

Most probably pigeons cannot fly faster than 70 ± 10 km. per hour, since at that rate heat regulation becomes a limiting factor. In a pigeon flying at this speed, the air sacs can be calculated to be almost completely emptied during each expiration.

The anatomy of the avian respiratory tract can only be understood, if we consider respiration as well as heat regulation during flight of a maximum intensity.

[1] cf. the summary p. 37—38.

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