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PAPER

LENGTH DENSITIES AND MINIMUM DIAMETER DISTRIBUTIONS OF THE AIR AND BLOOD CAPILLARIES OF THE PALEOPULMO AND NEOPULMO OF THE AVIAN LUNG

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ABSTRACT

The paleopulmo and neopulmo regions of the lungs of 5 mature wild Collared Turtle Dove (Streptopelia decaocto) have been analysed morphometrically. The number and the minimum diameters of the profiles of air and blood capillaries, and consequently their length densities, were estimated. Size distribution models were computed. The log normal fit of the air capillaries was better than that of the blood capillaries.

There were no significant differences in the diameters and length densities of the air and blood capillaries in the paleopulmo and neopulmo regions. It has been suggested that, contrary to the proposed functional differences in gas exchange capacities in the paleo- and neupulmo, there appear to be no differences in the dimensions of the gas exchange units in these two grossly distinct parts of the avian lung.

INTRODUCTION

Gas exchange in the avian lung takes place in the mantle of exchange tissue which surrounds the parabronchial lumen. As defined by the Nomina Anatomica Avium, the medio-ventral and mediodorsal secondary bronchi and their parabronchi largely comprise the paleopulmo, while the laterodorsal and lateroventral secondary bronchi and their parabronchi comprise the neopulmo (King, 1979).

In primitive birds, e.g. penguins, the paleopulmo comprises the whole lung. In the more advanced birds, e.g. passerine species, the neopulmo may comprise about one tenth of the volume of the lung. The air flow in the paleopulmo has been clearly shown by many authors (for a review, see

Scheid, 1979) to be unidirectional. In contrast it has been suggested (Duncker, 1971; Fedde, 1980; Brackenbury, 1981) that the air flow in the neopulmo changes with the phase of respiration.

Although a number of comprehensive quantitative studies on the avian lung have now been made (.e.g. Dubach, 1981; Abdalla *et al.*, 1982; Maina and King, 1982), the only quantitative observations on the exchange tissue of the paleopulmo and neopulmo regions of the avian lung appear to be a preliminary report by Maina (1982a) on the Collared Turtle Dove. The current study was an attempt to acquire further quantitative data on the paleo- and neopulmo to find out whether the gas exchange units in these two regions of the avian lung may be structurally different. The data acquired on this columbiform species of bird are compared with those of the relatively more energetic passeriform Common Starling (*Sturnis vulgaris*).

MATERIALS AND METHODS

Biological methods

The lungs of 5 adult Collared Turtle Doves (*Streptopelia decaocto*) were fixed *in situ* via the trachea by gravity with 2.3% glutaraldehyde buffered in sodium cacodylate to a pH of 7.4, total osmolarity 350 mOsmol. The subsequent tissue sampling and processing have been fully described by Abdalla *et al.*, (1982), Maina and King (1982) and Maina (1982a). Briefly this entailed cutting the lung into 4 slices along the costal sulci. Each slice was then transected into two unequal pieces by cutting just dorsomedial to the primary bronchus. The larger dorsomedial piece which was thus obtained was taken to represent the paleopulmo; the smaller ventrolateral piece, which terminates in the margo costo-septalis of the Nomina Anatomica Avium, represented the neopulmo. These two unequal pieces were diced and processed for electron microscopy by post-fixing in 2% osmium textroxide, block staining in uranyl acetate, dehydrating in ethanol, and embedding in Taab resin. One block was picked at random from the group derived from each half slice. Semi-thin sections (about 2 μm) stained with toluidine blue were used for estimation of the minimum diameters, and the number of profiles, of the air capillaries at x 2,000, using a calibrated graticule. The minimum diameters and number of profiles of the blood capillaries for each specimen were estimated on twenty-four stratified electron micrographs at x 7,500 (section thickness about 90 nm). The length densities of the air capillaries in these two regions were then estimated. In the analysis of these structural components the forbidden line principle (Gundersen, 1977) was observed, and sample size sufficiency was ascertained by the cumulative mean. In all about 1,600 profiles of the blood capillaries and about 3,500 of air capillaries were examined.

Mathematical methods

These are discussed in detail by Howard et al. (1980) and by Maina et al., (1981). The Students t-test was used for the analysis of the magnitudes of the parameters from the paleoneopulmo regions of the lung (Table 1).

RESULTS

Table 1. Mean length density (Lv) and minimum diameter (md) of the air capillaries (ac) and blood capillaries (bc) from the paleopulmo and neopulmo regions of the lungs of 5 Collared Turtle Doves (Streptopelia decaocto). Values are means (SD.)

Lv(ac)	$\mu m/\mu m^3$	0.0117	(0.0018)	0.0124	(0.0024)	NS
md(ac)	μm	6.63	(0.91)	6.86	(0.97)	NS
Lv(bc)	$\mu m/\mu m^3$	0.0182	(0.0020)	0.0204	(0.0019)	NS
md(bc)	μm	2.95	(0.18)	2.96	(0.24)	NS

DISCUSSION

Among the air breathing vertebrates the avian pulmonary design is unique. For reviews of the anatomy and physiology of the avian lung see King (1966), Duncker (1971), Schmidt--Nielsen (1975), Scheid (1979), and Brackenbury (1981). The parabronchi of the neopulmo anastomose much more profusely than those of the paleopulmo. Nevertheless it is not possible by studying the parabronchi in histological preparation, to distinguish with absolute certainty between these two regions of the avian lung.

It is now well established (for review see Scheid, 1979), that the airflow in the paleopulmo is continuous and uni-directional. That in the neopulmo has been claimed to oscillate with the phase of respiration (Duncker, 1971; Fedde, 1980; Brackenbury, 1981). Duncker (1971) suggested that gas exchange in the avian lung during resting breathing is confined to the neopulmo. This observation can now no longer be upheld as it has been observed (Holle et al., 1978) that the paleopulmo is as well ventilated as the neopulmo even during resting breathing. The functional significance of the neopulmo in the evolution of the avian lung is thus far from

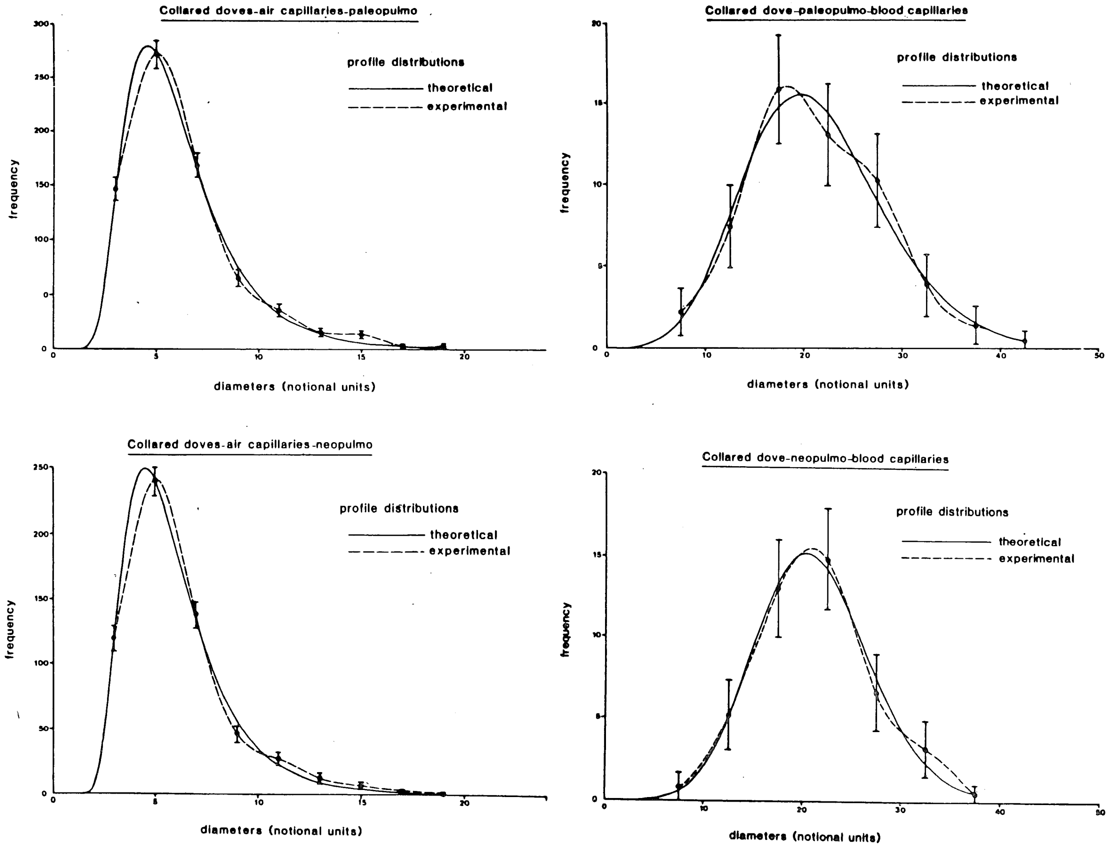

Figure 1. The size distributions of the blood capillaries and air capillaries in the paleopulmo and neopulmo regions of lung of the Collared Turtle Dove (*Streptopelia decaocto*).

being clearly understood.

The current study strongly suggests that there may not be structural differences in the components involved in gas exchange in the paleopulmo and neopulmo, as illustrated in Table 1.

The length density of the blood capillaries in the paleo- and neopulmo was higher than that of the air capillaries, the blood capillaries being much more numerous and smaller in diameter than the air capillaries. Such a relationship in the magnitudes of the length densities of air and blood capillaries was also observed for the lung of Sturnus vulgaris by Maina et al., (1981).

The fixatives used here cause minimal shrinkage. Any degree of shrinkage in any case should not bias the comparison of the sizes of the air- and blood capillaries in the paleo- and neopulmo regions of the lung. The effect of the estimat--ion of tubule or cylinder Lv on thick sections has been discussed in detail by Gundersen (1979). Errors inherent in using thick sections (as was done in this study for the air capillaries) would arise mainly from the fuzziness and overlap of the profiles. In our case the diameters of both air and blood capillaries were greater than the respective section thicknesses. Air and blood capillaries are extremely long, their total lengths being 15.3 km and 25.4 km respectively in the lung of the Common Starling (Sturnus vulgaris) (Maina et al., 1981), a bird of smaller size to the one examined in this study. The air and blood capillaries are also extremely tortuous structures (Maina 1982b). Where the cylinder or tubule length is relatively long (being greater than the sum of the profile minimal diameter, and section thickness) the bias in the estimation of Lv may be ignored (Gundersen, 1979). We thus do not expect much bias in the estimation of the diameters, and the length densities in the values reported in this paper.

The length densities of the blood capillaries and air capillaries in the much more energetic Sturnus vulgaris (Maina et al., 1981) are higher than those of the columbiform Streptopelia decaocto. This could be a form of adaptation in response to the higher relative oxygen consumption of the passeriform species (Lasiewski and Dawson, 1967). The diameters of the air capillaries in the lung of Sturnus vulgaris were smaller than those of the columbiform Strepto--pelia decaocto. It has been suggested (Weibel et al., 1981) that the partial pressure gradient, the driving force for oxygen, may depend on the diameter of the terminal airways. The relatively small diameter, i.e. high curvature, of the air capillaries in the lung of Sturnus vulgaris may therefore facilitate a relatively high partial pressure gradient for oxygen, and hence increase the diffusing capacity of the lung.

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REFERENCES

Abdalla MA, Maina JN, King AS, King DZ, Henry J. Morphometrics of the avian lung. 1. The domestic fowl (Gallus gallus variant domesticus). Respir Physiol 1982; 47: 267-278.

Brackenbury JH. Air flow and respired gases within the lung--air sac system of birds. Comp Biochem Physiol 1981; 68A: 1-8.

Dubach M. Quantitative analysis of the respiratory system of the House Sparrow, Budgerigar, and Violet-eared Hummingbird. Respir Physiol 1981; 46: 43-60.

Duncker H-R. The lung air sac system of birds. A contribution to the functional anatomy of the respiratory apparatus. Ergeb Anat Entwickl 1971; 45: 1-171.

Fedde MR. Structure and gas-flow pattern in the avian respiratory system. Poult Sci 1980; 59: 2642-2653.

Gundersen HJG. Notes on the estimation of the numerical density of arbitrary profiles: the edge effect. J Microsc 1977; 111: 219-223.

Gundersen, HJG. Estimation of tubule or cylinder Lv, Sc and Vv on thick sections. J Microsc 1979; 117: 333-345.

Holle JP, Heister N, Scheid P. Blood flow distribution in the duck lung and its control by respiratory gases. Am J Physiol 1978; 234: 146-154.

Howard CV, Scales LE, Lynch R. Numerical densities of alpha and gamma motor neurons in the trigeminal motor nucleus of the rat. A method of determining the separate numerical densities of two mixed populations of anatomic--ally similar cells. Microscopic (Wien) 1980; 37 (Suppl): 229-236.

King AS. Structural and functional aspects of the avian lungs and air sacs. Int Rev Gen Exp Zool 1966; 2: 171-267.

King AS. Systemia Respiratorium. In: Baumel JJ, King AS, Lucas AM, Breazile JE, Evans HE, eds. Nomina Anatomica Avium. London: Academic Press, 1979: 227-265.

Lasiewski RC and Dawson WR. A re-examination of the relation between standard metabolic rate and body weight in birds. The Condor 1967; 69: 12-23.

Maina JN, Howard CV, Scales L. The determination of the length densities and size distribution of blood and air capillaries in the avian lung involving a log normal fitting procedure. Sterol Yugoslav 1981; 3: 673-679.

Maina JN. A stereological analysis of the paleopulmo and neopulmo respiratory regions of the avian lung (Strepto-pelia decaocto. IRCS Medical Science 1982a; 10: 328.

Maina JN. A scanning electron microscopic study of the air and blood capillaries of the lung of the domestic fowl (Gallus domesticus). Experientia 1982b; 38: 614-616.

Maina JN, King AS. The thickness of the avian blood-gas barrier: qualitative and quantitative observations. J Anat 1982; 134: 553-562.

Scheid P. Mechanisms of gas exchange in birds. Rev Physiol Biochem Pharmacol 1979; 86: 137-186.

Schmidt-Nielsen K. Recent advances in avian respiration. In Peaker M, ed. Avian Physiology. London: Academic Press, 1975; 33-47.

Weibel ER, Taylor CR, Gehr H, Hoppeler H, Mathieu O, Maloiy GMO. Design of the mammalian respiratory system. IX. Functional and structural limits for oxygen flow. Respir Physiol 1981; 44: 151-164.