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Deficient anatomical capacity for oxygen uptake of the developing lung of the female domestic fowl when compared with the Red Jungle Fowl¹

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1. Introduction

The general embryonic development of the lung of the domestic fowl was established mainly by *Juillet* (1912), *Fox* and *Larsell* (1916 a, b), and *Duncker* (1978), and reviewed by *Romanoff* (1960). Qualitative ultrastructural studies on specialized aspects of the pre- and posthatching periods are also available (*Jones and Barson*, 1971; *Jones and Radnor*, 1972a, b). In contrast, no quantitative studies of the lung during either the pre- or posthatching development of the chick have been published for any species of bird. This is in contrast to the several quantitative works (*Burri and Weibel*, 1971; *Burri et al.*, 1974; *Hyde et al.*, 1977; *Pinkerton et al.*, 1982; and *Hislop et al.*, 1984) on the post-natal growth of the mammalian lung.

Quantitative observations by *Vidyadaran* (1986) have confirmed the discovery by *Maina* (1982) that the lung of the adult domestic fowl is far less well-adapted anatomically for gas exchange than that of the 25 non-galliform species which he investigated. Furthermore, stereological comparisons of the pulmonary anatomy of the adult female domestic fowl with that of its progenitor, the wild Red Jungle Fowl, by *Vidyadaran* (1986) and *Vidyadaran et al.* (1987) have disclosed that several major anatomical pulmonary parameters in the adult are substantially inferior functionally in the domestic fowl; thus the lung of the domestic fowl is about 20% smaller in volume when standardized against body weight, its blood-gas tissue barrier is about 28% thicker, and the anatomical diffusing capacity for oxygen of its blood-gas tissue barrier per kg body weight is about 25% lower, when compared with the lung of the adult Red Jungle Fowl. The gas exchange capacity of the lung of the Red Jungle Fowl has presumably been refined by natural selection (see *Vidyadaran et al.*, 1987, for discussion of the behavioural energetics of the wild Red Jungle Fowl), but these comparisons suggest that the lung of the

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domestic variant of this bird is much less well adapted for gas exchange than the lung of its wild ancestor. The adult female domestic fowl may now have a relatively reduced capacity to maintain an adequate oxygen uptake during additional stress such as heat, cold, humidity, altitude, or atmospheric pollution, with a consequent risk of hypoxaemia. There is now a world-wide incidence of ascites in young broilers, in which *Maxwell et al.* (1986a, b) have found widespread pathological changes closely resembling those which occur in hypoxic birds. *Julian and Wilson* (1986) and *Huchzermeyer and de Ruyck* (1986) have reported an association between the ascites and right ventricular hypertrophy, which could in turn be linked to chronic hypoxaemia. It was suggested by *Vidyadaran* (1986) and *Vidyadaran et al.* (1987) that selective breeding of the modern domestic fowl for earlier maturation and greater body weight has taken place in the absence of natural selection for respiratory adequacy.

The objective of this paper is to establish at what stage during posthatching development, and to what extent, the pulmonary stereological characteristics of the domestic fowl deviate from those of the Red Jungle Fowl.

2. Materials and Methods

Adult females and day old female chicks of a laying strain of birds (Euribred Hisex Brown) were obtained from a commercial poultry farm in England. The chicks were reared on a commercial brand of starter mash, and five were killed at each of days 1, 7, and 30, together with five adults which were in lay and over one year old. The eggs of wild Red Jungle Fowl (*Gallus gallus*) were collected from the Malaysian jungle and mature females were trapped. The eggs were incubated, the chicks were reared on similar starter mash, and five were killed at each of days 1, 7 and 30, with five adults.

Euthanasia was by an intraperitoneal injection of sodium pentobarbitone. The techniques of fixation of the lung, processing for light and electron microscopy under conditions of controlled osmolarity, uniformly random multistage sampling, and stereological analysis were the same as those described by *Abdalla et al.* (1982), *Maina and King* (1982), and *Maina* (1984). For the reasons given by *Abdalla et al.* (1982) and *Maina and King* (1982), it is believed that these procedures yield estimates of volumes, areas, and thicknesses of lung components, which are likely to represent approximately the values in life.

The anatomical diffusing capacities for oxygen of the components of the air-haemoglobin pathway were estimated from Weibel's (1970/71) model. The model distinguishes three components of this pathway, arranged in series, namely the tissue barrier comprising the combined epithelium of the air capillaries and the endothelium of the blood capillaries, the layer of blood plasma, and the erythrocytes themselves. In general, the diffusing capacity is directly proportional to the surface area of the barriers, inversely proportional to their thickness, and directly proportional to the volume of the blood in the capillaries of the lung. The tissue barrier and the plasma layer can be combined to form the so-called membrane component (D_{mo_2}). The parameters that can be estimated from the model are the diffusing capacity (conductance) for oxygen of the blood-gas tissue barrier (D_{to_2}), of the plasma layer (D_{po_2}), and of the erythrocytes (D_{eo_2}). The total anatomical diffusing capacity of all the barriers together (DL_{o_2}) can then be derived from the expression:

$$\frac{1}{DL_{o_2}} = \frac{1}{D_{to_2}} + \frac{1}{D_{po_2}} + \frac{1}{D_{eo_2}}$$

The values so obtained can be expressed as mlo_2 per minute, per mmHg, per kg body weight. The following physical coefficients are needed to calculate these diffusing capacities, i.e. K_{to_2} for the tissue barrier, K_{po_2} for the plasma, and Θ_{o_2} for the O_2 uptake by whole blood; the coefficients used were

those cited by *Weibel* (1970/71) for mammalian tissues, there being no equivalent coefficients for birds after hatching.

The venous haematocrit (Table 5) was measured on 5 domestic and 5 Red Jungle Fowl chicks at each of days, 1, 7, and 30. It was also measured in 5 adult female domestic fowl of the same strain as the chicks, and in 5 adult female Red Jungle Fowl. The value of Θ_{O_2} was adjusted by subtracting the volume of the nuclei of the erythrocytes (*Abdalla et al.*, 1982; *Maina and King*, 1982).

The data were analysed by a Model I fixed effects type of analysis of variance, normality of data, homogeneity of variances and non-adding being assumed, and the thickness of the blood-gas barrier was also examined by a Student's t-test.

The terminology for the structure of the avian lung follows the *Nomina Anatomica Avium* (*Baumel et al.*, 1979). Symbols are defined in Table 1.

3. Results

The body weights of the domestic fowl differed from those of the Red Jungle Fowl at the various ages as shown in Table 2. At day 1, the chick of the domestic fowl was twice the weight of the Red Jungle Fowl chick. The adult domestic fowl was about 52 times heavier than its day old chick; in contrast, the physically mature female Red Jungle Fowl was only 27 times heavier than its day old chick. The Red Jungle Fowl made very little weight gain between day 1 and day 7, but subsequently grew rapidly; between day 1 and day 7 the chicks of the domestic fowl tripled their body weights. In the Red Jungle Fowl, a 4.5 fold increase in body weight occurred between day 1 and day 30, but the domestic fowl increased its body weight 10 fold during the same period.

Table 1: Definition of symbols

De_{O_2}	oxygen diffusing capacity (conductance) of erythrocytes.
DL_{O_2}	total anatomical pulmonary diffusing capacity for oxygen.
Dm_{O_2}	anatomical diffusing capacity of the membrane for oxygen.
Dp_{O_2}	anatomical diffusing capacity of the plasma for oxygen.
Dt_{O_2}	anatomical diffusing capacity of the blood-gas (tissue) barrier for oxygen.
He	venous haematocrit.
Sa	surface area of the air capillary epithelium.
Sc	surface area of the blood capillary epithelium.
St	surface area of the blood-gas (tissue) barrier.
τ_{hp}	harmonic mean thickness of the plasma.
τ_{ht}	harmonic mean thickness of the blood-gas (tissue) barrier.
$\bar{\tau}$	arithmetic mean thickness of the blood-gas (tissue) barrier.
Va	volume of the lumen of the air capillaries.
Vb	volume of the wall and lumen of the blood vessels larger than capillaries.
Vc	volume of the lumen of the blood capillaries.
VL	volume of the fixed lungs (left lung $\times 2$)
Vlb	volume of the lumen of parabronchi and secondary bronchi (including atria).
Vp	volume of the wall and lumen of the primary bronchus.
Vt	volume of the tissue involved in gas exchange.
Vtn	volume of the tissue not involved in gas exchange.
Vx	volume of the exchange tissue of the lung.
W	body weight.

Weight-specific values are those standardized against body weight. For example VL/W is the weight-specific lung volume.

The weight-specific volume of the lung (i.e. the lung volume per unit body weight, VL/W, Table 2) of the domestic fowl at day 1 was significantly larger ($P < 0.05$) than in the adult. At day 7 it was much smaller than at day 1 ($P < 0.01$), day 30 ($P < 0.05$), and in the adult ($P < 0.05$). These relationships were almost reversed in the Red Jungle Fowl, where the value for day 7 was not significantly different from day 1, and was much larger than at day 30 ($P < 0.01$) and in the adult ($P < 0.01$). Age for age comparisons of the weight-specific volumes of the lung of the domestic fowl with those of the Red Jungle Fowl (Table 2) indicate that at day 1 ($P < 0.05$), day 7 ($P < 0.01$), and in the adult ($P < 0.05$), the values for the domestic fowl were significantly smaller than those of the Red Jungle Fowl. A striking observation is that the weight-specific volume of the lung at day 7 was so remarkably low in the domestic fowl ($10.59 \text{ mm}^3/\text{g}$, Table 2). This indicates that the rapid increase in the body weight of the domestic fowl that occurred by day 7 had not been matched by anything like a proportional increase in lung volume.

The relative and absolute volumes of the four main components of the lung are shown in Table 3. The two components with the largest volumes are the exchange tissue (V_x) and the combined lumens of the parabronchi and secondary bronchi (V_{1b}). Table 5 shows that the weight-specific volumes of these components, V_x/W and V_{1b}/W , in the domestic fowl were lower at day 7 than in the three other age groups ($P < 0.01$). On the other hand in the Red Jungle Fowl the values for these two components were highest at day 7. Age for age, both of these components were higher in the Red Jungle Fowl than in the domestic fowl, V_x/W at day 7 being 2.3 times higher ($P < 0.01$).

The relative and absolute volumes of the main components of the exchange tissue are summarized in Table 4. The two most important of these are the volume of the blood capillaries (V_c) and volume of the air capillaries (V_a), and the weight-specific volumes of these (V_c/W and V_a/W) are shown in Table 5. In the domestic fowl the values for V_c/W were significantly lower ($p < 0.01$) at days 7 and 30 than at day 1 and in the adult.

Table 2: Means and standard deviations of body weight and lung volume of female chicks and adults of domestic fowl and Red Jungle Fowl. The values for volumes pertain to the combined right and left fixed lungs

	n	Body weight (W) kg	Lung volume (VL) cm ³	Lung volume per unit body weight mm ³ /g
<i>domestic fowl</i>				
day 1	5	0.0358 ± 0.003	0.65 ± 0.03	18.30 ± 1.62
day 7	5	0.1198 ± 0.009	1.28 ± 0.20	10.59 ± 0.93
day 30	5	0.3670 ± 0.070	5.79 ± 1.11	15.81 ± 0.57
Adult	5	1.8728 ± 0.355	26.59 ± 2.10	14.65 ± 3.17
<i>Red Jungle Fowl</i>				
day 1	5	0.0174 ± 0.003	0.39 ± 0.07	22.49 ± 2.69
day 7	5	0.0185 ± 0.002	0.48 ± 0.09	25.81 ± 2.80
day 30	5	0.0798 ± 0.016	1.40 ± 0.44	17.18 ± 2.69
Adult	5	0.4781 ± 0.069	8.71 ± 1.91	18.10 ± 1.94

Table 3: Means and standard deviations of relative and absolute volumes of main components of the lungs of female chicks of domestic fowl and Red Jungle Fowl. The absolute volumes pertain to the combined volumes of the right and left fixed lungs

n	Exchange tissue (Vx)		Lumen of parabronchi and secondary bronchi (Vlb)		Blood vessels larger than capillaries (Vb)		Primary bronchus (VP)	
	relative %	absolute cm ³	relative %	absolute cm ³	relative %	absolute cm ³	relative %	absolute cm ³
<i>domestic fowl</i>								
5	54.12 ± 1.17	0.353 ± 0.02	33.56 ± 2.45	0.219 ± 0.03	5.67 ± 0.71	0.037 ± 0.00	6.64 ± 1.15	0.043 ± 0.01
5	53.72 ± 1.75	0.678 ± 0.12	35.30 ± 1.73	0.451 ± 0.08	6.59 ± 1.10	0.084 ± 0.02	4.39 ± 1.22	0.054 ± 0.01
5	51.21 ± 0.84	2.963 ± 0.56	39.19 ± 1.50	2.262 ± 0.39	5.79 ± 1.08	0.344 ± 0.13	3.82 ± 1.08	0.219 ± 0.07
5	49.66 ± 0.88	13.216 ± 1.23	38.01 ± 0.98	10.108 ± 0.83	6.64 ± 0.64	1.769 ± 0.25	5.69 ± 1.02	1.496 ± 0.22
<i>Red Jungle fowl</i>								
5	53.09 ± 1.81	0.194 ± 0.03	37.00 ± 0.06	0.135 ± 0.02	4.49 ± 0.33	0.017 ± 0.00	5.42 ± 2.06	0.020 ± 0.01
5	51.22 ± 1.51	0.245 ± 0.04	40.67 ± 1.69	0.195 ± 0.04	4.52 ± 1.71	0.022 ± 0.01	3.60 ± 0.80	0.018 ± 0.01
5	53.47 ± 1.16	0.744 ± 0.23	36.34 ± 3.31	0.507 ± 0.16	5.86 ± 1.48	0.081 ± 0.03	4.32 ± 1.53	0.064 ± 0.04
5	53.15 ± 1.49	4.607 ± 0.88	36.05 ± 1.72	3.156 ± 0.80	6.16 ± 1.46	0.540 ± 0.18	4.63 ± 0.41	0.405 ± 0.11

Table 4: Means and standard deviations of relative and absolute volumes of the exchange tissue of the lungs of female chicks of domestic fowl and Red Jungle Fowl. The absolute volumes pertain to the combined volumes of the right and left fixed lungs

n	Blood capillaries (VC)		Air capillaries (Va)		Tissue of the blood-gas (tissue) barrier (Vt)		Tissue not involved in gas exchange (Vtn)	
	relative %	absolute cm ³	relative %	absolute cm ³	relative %	absolute cm ³	relative %	absolute cm ³
<i>domestic fowl</i>								
5	22.79 ± 4.06	0.081 ± 0.02	46.57 ± 3.04	0.164 ± 0.01	9.30 ± 1.77	0.033 ± 0.01	21.34 ± 3.23	0.075 ± 0.01
5	17.91 ± 3.16	0.124 ± 0.03	55.06 ± 3.94	0.375 ± 0.05	9.65 ± 1.37	0.066 ± 0.02	17.39 ± 1.45	0.121 ± 0.03
5	19.55 ± 2.60	0.569 ± 0.05	55.09 ± 1.68	1.637 ± 0.34	9.82 ± 0.75	0.291 ± 0.06	15.54 ± 2.19	0.466 ± 0.15
5	27.89 ± 2.77	3.701 ± 0.60	55.59 ± 0.66	7.344 ± 0.68	7.44 ± 0.65	0.972 ± 0.13	9.09 ± 2.33	1.191 ± 0.27
<i>Red Jungle Fowl</i>								
5	25.09 ± 6.52	0.050 ± 0.02	47.30 ± 6.78	0.091 ± 0.01	8.21 ± 0.87	0.16 ± 0.00	19.39 ± 2.47	0.038 ± 0.01
5	21.07 ± 1.22	0.052 ± 0.01	52.28 ± 4.85	0.129 ± 0.03	8.24 ± 0.70	0.020 ± 0.00	18.41 ± 3.26	0.045 ± 0.01
5	16.77 ± 4.98	0.128 ± 0.06	59.40 ± 4.11	0.440 ± 0.14	7.68 ± 0.87	0.057 ± 0.02	16.14 ± 3.78	0.120 ± 0.05
5	21.29 ± 2.45	0.980 ± 0.22	64.82 ± 4.83	2.984 ± 0.62	6.01 ± 0.32	0.277 ± 0.06	7.88 ± 2.19	0.365 ± 0.13

Table 5: The blood-gas barrier. Ratios of surface to body weight and surface to volume; thicknesses of barriers; anatomical diffusing capacity for oxygen. Mean values \pm standard deviation. All lung values except those of thickness pertain to the combined right and left fixed lungs

W	units	Domestic Fowl				Red Jungle Fowl				adults
		day 1	day 7	day 30	adults	day 1	day 7	day 30	adults	
	kg	0.0358 \pm 0.003	0.1198 \pm 0.009	0.3670 \pm 0.070	1.8728 \pm 0.355	0.0174 \pm 0.003	0.0185 \pm 0.002	0.0798 \pm 0.016	0.4781 \pm 0.069	
VL	cm ³	0.65 \pm 0.03	1.28 \pm 0.20	5.79 \pm 1.11	26.59 \pm 2.10	0.39 \pm 0.07	0.48 \pm 0.09	1.46 \pm 0.44	8.71 \pm 1.91	
VL/W	mm ³ /g	18.30 \pm 1.62	10.59 \pm 0.93	15.81 \pm 0.57	14.65 \pm 3.17	22.49 \pm 2.69	25.81 \pm 2.80	17.18 \pm 2.69	18.10 \pm 1.94	
Vx/W	cm ² /g	9.91 \pm 0.86	5.69 \pm 0.60	8.09 \pm 0.25	7.29 \pm 1.69	11.25 \pm 2.01	13.21 \pm 1.30	9.18 \pm 1.41	9.61 \pm 0.92	
Vlb/W	cm ² /g	6.15 \pm 0.81	3.74 \pm 0.43	6.19 \pm 0.30	5.59 \pm 1.23	7.87 \pm 1.50	10.47 \pm 0.97	6.23 \pm 0.99	6.54 \pm 0.93	
Vc/W	cm ² /g	2.25 \pm 0.32	1.03 \pm 0.23	1.58 \pm 0.22	2.07 \pm 0.64	2.87 \pm 1.20	2.80 \pm 0.34	1.57 \pm 0.61	2.06 \pm 0.42	
Va/W	cm ² /g	4.61 \pm 0.55	3.12 \pm 0.24	4.46 \pm 0.13	4.06 \pm 0.97	5.24 \pm 0.67	6.93 \pm 0.78	5.48 \pm 0.84	6.21 \pm 0.41	
Sa/W	cm ² /g	26.0 \pm 3.61	13.05 \pm 1.49	16.15 \pm 2.29	18.08 \pm 2.51	21.89 \pm 3.56	31.33 \pm 2.37	19.80 \pm 3.58	20.24 \pm 2.81	
St/W	cm ² /g	14.88 \pm 2.18	7.49 \pm 1.16	10.17 \pm 1.98	12.46 \pm 1.96	13.65 \pm 2.09	18.32 \pm 1.42	10.76 \pm 3.77	12.97 \pm 1.59	
Sc/W	cm ² /g	19.51 \pm 2.38	9.42 \pm 1.45	13.67 \pm 2.07	14.82 \pm 2.64	19.92 \pm 3.56	23.31 \pm 2.75	13.39 \pm 4.01	15.40 \pm 1.94	
St/Vx	m ² /m ³	149.79 \pm 13.24	132.11 \pm 18.62	125.98 \pm 26.10	172.84 \pm 12.45	126.12 \pm 23.52	139.45 \pm 8.75	116.45 \pm 30.69	135.17 \pm 13.54	
rht	μ m	0.462 \pm 0.02	0.521 \pm 0.04	0.485 \pm 0.08	0.322 \pm 0.01	0.419 \pm 0.03	0.385 \pm 0.05	0.316 \pm 0.06	0.252 \pm 0.02	
rhp	μ m	0.378 \pm 0.01	0.636 \pm 0.15	0.622 \pm 0.16	0.300 \pm 0.06	0.442 \pm 0.08	0.429 \pm 0.05	0.504 \pm 0.07	0.463 \pm 0.07	
\bar{r}	μ m	0.622 \pm 0.05	0.619 \pm 0.09	0.573 \pm 0.06	0.459 \pm 0.11	0.610 \pm 0.14	0.615 \pm 0.03	0.639 \pm 0.09	0.452 \pm 0.05	
\bar{r} /rht	μ m/ μ m	1.35 \pm 0.13	1.19 \pm 0.16	1.19 \pm 0.10	1.44 \pm 0.37	1.46 \pm 0.32	1.62 \pm 0.22	2.08 \pm 0.48	1.79 \pm 0.17	
He	%	24.75	24.20	29.80	27.07	24.30	29.20	28.60	28.20	
Dt _{o2} /W	ml _{o2} /min/mmHg/kg	10.72 \pm 1.35	4.76 \pm 0.63	7.27 \pm 2.70	12.79 \pm 2.20	11.11 \pm 2.03	15.96 \pm 2.57	11.23 \pm 2.91	17.01 \pm 1.95	
Dp _{o2} /W	ml _{o2} /min/mmHg/kg	23.42 \pm 5.35	6.39 \pm 2.47	10.30 \pm 4.20	19.31 \pm 2.49	22.39 \pm 7.79	24.25 \pm 2.30	10.96 \pm 4.00	13.55 \pm 2.69	
De _{o2} /W	ml _{o2} /min/mmHg/kg	1.82 \pm 0.25	0.80 \pm 0.15	1.49 \pm 0.21	1.76 \pm 0.52	2.46 \pm 0.85	2.58 \pm 0.46	1.42 \pm 0.57	1.81 \pm 0.37	
Dm _{o2} /W	ml _{o2} /min/mmHg/kg	7.04 \pm 0.69	2.64 \pm 0.59	4.22 \pm 1.62	7.61 \pm 1.03	7.50 \pm 1.43	9.70 \pm 1.25	5.51 \pm 1.61	7.48 \pm 1.12	
DL _{o2} /W	ml _{o2} /min/mm Hg/kg	1.52 \pm 0.13	0.62 \pm 0.08	1.05 \pm 0.18	1.39 \pm 0.36	2.01 \pm 0.51	2.04 \pm 0.48	1.08 \pm 0.37	1.42 \pm 0.25	

There was a significant difference ($P < 0.01$) between the values for V_c/W in the domestic fowl and Red Jungle Fowl at day 7 only, that for the Red Jungle Fowl being 2.7 times higher. In other words at day 7 the lung of the domestic fowl has relatively much less blood than that of the Red Jungle Fowl. In the domestic fowl there were no significant differences in V_a/W between day 1, day 20, and the adult, but the value at day 7 was significantly lower ($P < 0.01$) than at the other three ages. In the Red Jungle Fowl the highest value for V_a/W was observed at day 7, and the value at this age was more than twice that in the domestic fowl. These observations on V_c/W and V_a/W support the view that in the domestic fowl the lung growth had fallen far behind the growth of the body at day 7.

The weight-specific surface areas of the resistance barriers of the air-haemoglobin pathway are given in Table 5. That of the blood-gas (tissue) barrier (St/W) in the domestic fowl at day 7 was significantly lower ($P < 0.01$) than at the other three ages, but in the Red Jungle Fowl it was significantly higher ($P < 0.01$) at day 7 than at all other ages. The value at day 7 for the Red Jungle Fowl was 2.5 times greater than that for the domestic fowl. There was no significant difference between the two birds at the three other ages.

The surface density of the blood-gas tissue barrier (i.e. the surface area per unit volume of exchange tissue, St/V_x) tended in general to be greater in the domestic fowl than in the Red Jungle Fowl from day 1 onwards (Table 5). In other words the developing domestic fowl packs a relatively greater surface area for gas exchange into its exchange tissue than does the Red Jungle Fowl.

The harmonic mean thickness of the blood-gas (tissue) barrier (τ_{ht} , Table 5) in the adult was significantly thinner than that of the chicks at days 1, 7 and 30 in both the domestic fowl and the Red Jungle Fowl ($P < 0.01$ for the domestic fowl, and also for the Red Jungle Fowl except at day 30 when $P < 0.05$). However, some important differences were noted between the domestic fowl and Red Jungle Fowl. In the Red Jungle Fowl the barrier became progressively thinner from day 1 till adulthood; in the domestic fowl it actually grew thicker between day 1 and day 7, and at day 30 was still as thick as at day 1. Furthermore, the barrier was thicker in the domestic fowl than in the Red Jungle Fowl at all ages ($P < 0.05$ at day 1, and < 0.01 elsewhere).

The harmonic mean thickness of the plasma (τ_{hp}) is a dubious parameter because it attempts to measure the moving blood stream (Perry, 1978), but it is given in Table 5 since it contributes to the total anatomical diffusing capacity (DL_{O_2}) of Weibel's model. The arithmetic mean thickness of the tissue barrier ($\bar{\tau}_t$) is also included in Table 5 since it reflects the mass, and hence the oxygen consumption, of the tissues which form the barrier; it varied little between the domestic fowl and Red Jungle Fowl.

The weight-specific anatomical diffusing capacity for oxygen of the tissue barrier (D_{to_2}/W , Table 5) of the domestic fowl at day 7 was significantly lower than at the three other ages ($P < 0.01$, but 0.05 when compared with day 30). In contrast, in the Red Jungle Fowl it was significantly higher ($P < 0.01$) at day 7 than at days 1 and 30. Comparison of the D_{to_2}/W between the domestic fowl and the Red Jungle Fowl showed that the value was slightly lower in the domestic fowl at day 1, but the difference was not significant; the values for the Red Jungle Fowl were significantly higher than those of the

domestic fowl at the other three ages ($P < 0.01$ at day 7 otherwise < 0.05). This shows that the all-important weight-specific oxygen diffusing capacity of the blood-gas (tissue) barrier in the domestic fowl is inferior to that of the Red Jungle Fowl from day 7 up to, and including, the adult. In other words, the lung at day 1 is almost as well adapted for gas exchange in the domestic fowl as in the Red Jungle Fowl, but subsequently the lungs of the domestic fowl become much less adequate relative to body weight than those of the Red Jungle Fowl, and especially at day 7.

The mean weight-specific total anatomical diffusing capacity (DL_{O_2}/W) expresses the diffusing capacity of oxygen through all of the three resistance barriers in Weibel's model, thus taking into account D_{tO_2} , D_{pO_2} , and D_{eO_2} (Table 5). In the domestic fowl, DL_{O_2}/W was significantly lower at day 7 than in the three other age groups ($P < 0.01$). These values are given in Table 5, but since D_{lO_2} includes D_{pO_2} it is influenced by the harmonic mean thickness of the plasma layer (τ_{hp}), which is an inconstant parameter as already stated. D_{mO_2} also includes D_{pO_2} , but D_{tO_2} does not. For that reason D_{tO_2} is the most meaningful of these conductances. However, as Table 5 shows, at day 7 in the domestic fowl the weight-specific DL_{O_2} , D_{pO_2} , and D_{mO_2} are all relatively very low. So also is D_{eO_2} , which reflects the uptake of oxygen by the erythrocytes. In Weibel's model, D_{eO_2} takes account of the volume of capillary blood in the lung (V_c), and a low D_{eO_2} is therefore predictable from the low weight-specific volume of capillary blood, V_c/W , in the domestic fowl at day 7 (Table 5).

4. Discussion

Comparison of the pulmonary stereological characteristics of the posthatching stages of the domestic fowl with those of the wild Red Jungle Fowl have shown that, at day 7, all parameters are extremely unfavourable to the domestic fowl. These include the three parameters that most directly affect the weight-specific anatomical diffusing capacity for oxygen of the blood-gas tissue barrier: thus the value of the weight-specific surface area of the tissue barrier (St/W) of the domestic fowl at day 7 is only about 41% of that of the Red Jungle fowl; the weight-specific pulmonary capillary blood volume (V_c/W) of the domestic fowl was only about 37% of that of the Red Jungle Fowl; and, even more remarkably, at day 7 the harmonic mean thickness of the blood-gas tissue barrier was 35% thicker in the domestic fowl than in the Red Jungle Fowl. Moreover in the Red Jungle Fowl the tissue barrier became progressively thinner from day one to adulthood, but in the domestic fowl it actually became thicker between day 1 and day 7, and at day 30 it was still almost as thick as it was at day 1. The values for the thickness of the barrier at day 1 in the two birds are of particular interest. At this stage the barrier was about 10% thicker in the domestic fowl than in the Red Jungle Fowl, the difference being just significant ($P < 0.05$); this observation should be checked by further measurements. The weight-specific anatomical diffusing capacity of the blood-gas tissue barrier for oxygen (D_{tO_2}/W) of the domestic fowl at day 7 was only 30% of that of the Red Jungle Fowl of the same age. This parameter expresses the maximum amount of oxygen that the tissue barrier can diffuse in unit time per unit body weight, assuming that perfect ventilation is matched by perfect perfusion. It therefore reveals the ultimate

functional limit of the epithelial-endothelial barrier for gas exchange. The relatively low value in the domestic fowl suggests a quite profound respiratory inadequacy which could restrict the capacity of the chick to compensate for extraneous stress such as cold, altitude, or air pollution.

Therefore the chick of the domestic fowl evidently encounters a crisis in its respiratory development shortly after hatching. However, the deficiency of the lung is not confined to day 7. In our observations the blood-gas (tissue) barrier in the domestic fowl was significantly thicker than that of the Red Jungle Fowl from day 1 through to adulthood. Likewise, the weight-specific anatomical diffusing capacity of the tissue barrier for oxygen was significantly lower in the domestic fowl than in the Red Jungle Fowl not only at day 7 but also at day 30 and in the adult.

Almost all of these findings can be attributed to the much faster increase in body weight in the domestic fowl than in the Red Jungle Fowl. In the domestic fowl the development of the lung fails to keep up with the growth of the body, particularly in the first few days after hatching. The energetic demands of such rapid growth presumably reduce still further the respiratory reserves needed to deal with any additional stress. The relatively greater thickness of the blood-gas barrier in the chicks of the domestic fowl cannot, however, be blamed on growth rate. This could presumably be of pathological origin, in response to infection or atmospheric pollution. However, the slightly greater thickness of the barrier at day 1 in the domestic fowl than in the Red Jungle Fowl (if confirmed) is unlikely to be of pathological origin and may point to a genetic change which has crept in unnoticed during the selection for early maturation.

Finally it should be noted that these observations emphasise day 7 after hatching, but we have no information about the stereological parameters of the lung between day 7 and day 30, and this period needs investigation.

Summary

A comprehensive stereological comparison has been made of the anatomy of the lungs of the domestic fowl with that of its wild progenitor, the Red Jungle Fowl, in 1 day, 7 day, 30 day, and adult female birds. All lung parameters, when standardized against body weight, were extremely unfavourable to the domestic fowl at day 7. The surface area of the blood-gas tissue barrier was only about 41% of that of the Red Jungle Fowl, the volume of pulmonary capillary blood was only about 37% of that of the Red Jungle Fowl, and the harmonic mean thickness of the tissue barrier was about 35% thicker in the domestic fowl; consequently the anatomical diffusing capacity of the tissue barrier for oxygen was only about 30% of that of the Red Jungle Fowl. Pulmonary deficiencies were not restricted to day 7. The tissue barrier was significantly thicker in the domestic fowl than in the Red Jungle Fowl from day 1 through to adulthood. The anatomical diffusing capacity for oxygen per unit body weight was significantly lower in the domestic fowl not only at day 7 but also at day 30 and in the adult.

All but one of these anatomical deficiencies can be attributed to the much faster growth rate of the domestic fowl, which has completely outrun the development of the lungs and in so doing may have reduced the respiratory reserves needed by the chick to deal with any additional stress. The increased thickness of the blood-gas tissue barrier cannot be attributed to the excessive growth rate, and seems more likely to be of genetic than pathological origin.

Zusammenfassung

Es wurde eine umfassende stereologische Vergleichsstudie der Lungenanatomie des Haushuhnes gegenüber jener seines wilden Vorfahren, des Roten Dschungelhuhnes, angestellt und zwar am 1., 7.

und 30. Lebenstag sowie an ausgewachsenen weiblichen Tieren. Alle Lungenparameter, standardisiert auf das Körpergewicht, waren ausserordentlich ungünstig für das 7tägige Haushuhn. Die Oberfläche der Blut-Gas-Gewebeschranke war nur etwa 41% und das Volumen des Lungenkapillarblutes nur etwa 37% der Werte beim Roten Dschungelhuhn, und das harmonische Mittel der Dicke der Gewebebarriere war beim Haushuhn um etwa 35% grösser. Folglich betrug die anatomische Diffusionskapazität der Gewebebarriere für Sauerstoff nur etwa 30% von jener des Roten Dschungelhuhnes. Dieses Ungenügen der Lungen blieb nicht auf den 7. Lebenstag beschränkt. Die Gewebebarriere war beim Haushuhn signifikant dicker vom 1. Lebenstag bis zum Erwachsenenalter. Die anatomische Diffusionskapazität für Sauerstoff per Einheit Körpergewicht war beim Haushuhn signifikant geringer, nicht nur am 7., sondern auch am 30. Tag und beim Erwachsenen.

Mit einer Ausnahme können alle diese anatomischen Unzulänglichkeiten der viel schnelleren Wachstumsrate des Haushuhnes zugeschrieben werden, die die Lungenentwicklung vollständig hinter sich gelassen hat und derart die Atmungsreserven verringert haben mag, die das Huhn benötigen würde, um mit irgendwelchen zusätzlichen Belastungen fertigzuwerden.

Die grössere Dicke der Blut-Gas-Gewebebarriere jedoch kann nicht der übermässigen Wachstumsrate zugeschrieben werden, sondern scheint eher eine genetische als eine pathologische Grundlage zu haben.

Résumé

On a procédé à une étude stéréologique globale en comparant l'anatomie du poumon de la poule domestique à celle de son ancêtre sauvage la poule de Java. Ont été examinées les femelles âgées de 1, 7, 30 jours, et adultes. Tous les paramètres des poumons, standardisés selon le poids corporel, étaient extrêmement défavorables pour la poule domestique de 7 jours. La surface de la barrière sang-gaz ne représentait qu'environ 41%, le volume de sang pulmonaire capillaire qu'environ 37% des valeurs observées chez la poule de Java, et la moyenne harmonique de l'épaisseur de la barrière tissulaire était plus grande d'environ 35% chez la poule domestique. Par conséquent, pour l'oxygène, la capacité anatomique de diffusion de la barrière tissulaire n'atteignait que 30% de celle de la poule de Java. Cette insuffisance pulmonaire n'était pas limitée à ce 7^{ème} jour. Chez la poule domestique, la barrière tissulaire était plus épaisse de façon significative dès le premier jour jusqu'à l'âge adulte; la capacité de diffusion anatomique de l'oxygène par unité de poids corporel était inférieure de façon significative non seulement le 7^{ème}, mais aussi le 30^{ème} jour, et chez l'adulte.

A l'exception d'une, toutes ces insuffisances anatomiques peuvent être attribuées au taux de croissance beaucoup plus rapide de la poule domestique. Celui-ci a complètement laissé de côté le développement pulmonaire et peut avoir réduit les réserves respiratoires au point que la poule ne peut plus assumer la moindre charge supplémentaire.

L'épaisseur plus grande de la barrière sang-gaz ne peut, elle, être imputée au taux de croissance excessif, mais semble provenir d'une cause génétique plutôt que pathologique.

Riassunto

Venne effettuato un completo studio stereologico della anatomia del polmone del pollo domestico, comparato a quella del suo predecessore, il pollo rosso della giungla. Vennero raffrontati polli di sesso femminile al primo, settimo e trentesimo giorno di vita ed allo stato adulto. Tutti i parametri dei polmoni, standardizzati secondo il peso corporeo, furono molto sfavorevoli per i polli al settimo giorno d'età. La superficie della barriera sangue-gas-tessuto era solo del 41%, il volume del sangue dei capillari polmonari solo del 37% dei valori individuati nel pollo rosso della giungla, mentre l'armonica media dello spessore della barriera tissulare nel pollo domestico era superiore del 35%.

Di conseguenza la capacità anatomica di diffusione della barriera tissulare per l'ossigeno raggiungeva solo il 30% di quella del pollo rosso della giungla. Questo dato sfavorevole dei polmoni non rimase legato al pollo di sette giorni d'età. La barriera tissulare nel pollo domestico fu più densa in modo significativo dal primo giorno di vita fino all'età adulta. La capacità anatomica di diffusione dell'ossigeno per unità di peso corporeo nel pollo domestico risultò sensibilmente più piccola non solo al settimo giorno ma anche al trentesimo e nel pollo adulto.

Con una eccezione tutte queste inammissibilità anatomiche ascrivibili alla molto più rapida quota di crescita del pollo domestico, hanno lasciato totalmente in ritardo lo sviluppo del polmone e con ciò hanno diminuito le riserve della respirazione, delle quali dovrebbe disporre il pollo per venire a capo di qualsiasi maggior carico. Il maggior spessore della barriera tissulare del sangue-gas non può esser ascritto alla maggior quota di crescita, ma appare avere maggiormente una base genetica che patologica.

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PERSONELLES

Prof. Dr. Gottlieb Flückiger, Bern, 95jährig

In Bern begeht am 13. Juni 1987 Prof. Dr. G. *Flückiger*, ehemaliger Direktor des eidgen. Veterinärarnes (1932–1957) den 95. Geburtstag. Seit Jahren an den Beschwerden des hohen Alters leidend, in seine vier Wände gebunden, genießt er doch das Privileg des «Bei sich zu Hause seins» und der Kommunikation mit der Aussenwelt, soweit er diese wünscht.

Prof. *Flückiger* ist heute – nach dem Hinschied von Dr. Ernst *Augsburger* – das älteste Mitglied der einstigen Absolventen der bernischen tierärztlichen Fakultät. Er bestand sein Staatsexamen im März 1918, kurz vor dem Tode Prof. *Guillebeau's*, und als Prof. E. *Hess* noch im Amt war.

Er ist aber nicht nur das älteste Mitglied, sondern auch der Gründer und Initiator einer Vereinigung, die zwar wenig Lärm um sich macht, aber eine wichtige Funktion erfüllt und bisher alle Höhen und Tiefen überlebt hat: charakteristischerweise «Les Vétérans de Berne» genannt, ist sie eine lockere Verbindung aller, die in Bern ihr Berufsdiplom vor 20 und mehr Jahren erworben haben. Man versammelt sich einmal im Jahr («man» heisst etwa die Hälfte der Registrierten) zu einem Mittagessen in Bern, die geringen «Verwaltungskosten» werden durch Hutsammlung zwischen Dessert und Kaffee gedeckt, und Spiritus rector ist zur Zeit Dr. Jean *Staehli*, rue de la Chapelle 44, 2035 Corcelles NE.

Es wäre zu hoffen, dass immer mehr ehemalige bernische Absolventen sich dieses Gremiums erinnern wollten, nicht nur aus alter Treue zu ihrer alma mater, aber besonders auch – und dies war und ist das zentrale Anliegen von G. *Flückiger* – damit der berühmt-berüchtigte Graben zwischen Romands und Alémaniques, soweit es uns Tierärzte betrifft, ein Un-Ding bleibe oder werde. In Zukunft dürfte dieser Aspekt immer mehr Bedeutung erlangen.

In den letzten Jahren sind – soweit der Schreibende informiert ist – die Kollegen E. *Augsburger*, M. *Denner*, H. *Fleischlin*, J. *Good*, P. von *Grünigen*, A. *Hodel*, H. *Hofstetter*, P. *Kästli*, A. *Leu*, J. *Pidoux*, J. *Stirnemann*, K. *Weder*, E. *Wenger*, A. *Zbinden* und W. *Zürcher* von uns gegangen, sowie E. *Bourgeois* (Staats Juli 1925, gest. 1986). Auf unserer Liste fehlt auch M. *Kamm* (Staats 1923; früher in Huttwil).

Möge Prof. *Flückiger* diese kleine Flurbereinigung als Dedicatio zu seinem hohen Geburtstag auffassen!

R. F., B.