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RELATIONSHIP BETWEEN HAEMOGLOBIN O_2 AFFINITY AND THE VENTILATORY RESPONSE TO HYPOXIA IN THE RHEA AND PHEASANT

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The ventilatory response to hypoxia appears to be controlled largely by carotid body chemoreceptors in birds, as it is in mammals, and the stimulus to these chemoreceptors is probably the partial pressure of oxygen in the arterial blood (Bouverot, 1978; Bouverot, Douguet & Sebert, 1979). There are, however, interspecific differences in the threshold arterial P_{O_2} stimulating the hypoxic ventilatory response. Black & Tenney (1980) found that a high-altitude species, the bar-headed goose, initiates an increase in ventilation at a lower arterial P_{O_2} (Pa_{O_2}) than a lowland species, the Pekin duck. The bar-headed goose also has a higher affinity haemoglobin, presumably as an adaptation to its high altitude habitat. Van Nice, Black & Tenney (1980) noted that when the ventilatory response to hypoxia is expressed in terms of the percent saturation of haemoglobin in arterial blood (Sa_{O_2}), the bar-headed goose and Pekin duck exhibit a similar threshold Sa_{O_2}. It seems unlikely that the receptors sense haemoglobin O_2 saturation directly and experimental reductions in O_2 content do not stimulate ventilation in the duck (D. F. Boggs, unpublished observation). Nonetheless a relationship between the threshold of the ventilatory response to hypoxia and the 'knee' of the oxyhaemoglobin dissociation curve would be a reasonable evolutionary development in both birds and mammals, as Van Nice *et al.* (1980) have pointed out. If threshold arterial P_{O_2} for the hypoxic ventilatory response were an interspecific constant, then those species with relatively high-affinity haemoglobins would be responding prematurely, and, therefore, 'wastefully', whereas those with relatively low-affinity haemoglobins would be in danger of suffering substantial arterial unsaturation before the ventilatory response is initiated. The latter eventuality would be particularly hazardous for tissue oxygen supply in those animals with low affinity haemoglobins, since these animals are in most cases small, with high weight-specific metabolic rates (Lutz, Longmuir & Schmidt-Nielsen, 1974; Schmidt-Nielsen & Larimer, 1958).

To examine this question, we investigated the hypoxic ventilatory response in the rhea (*Rhea americana*), which has a relatively high-affinity haemoglobin (Lutz *et al.* 1974), and in the ring-necked pheasant (*Phasianus colchicus*), in which the affinity is substantially lower. This species of rhea does not live at particularly high altitude, in its native Argentine and Brazilian grasslands, so its ventilatory response should not, in itself, represent an aspect of hypoxic adaptation, as may be the case in the bar-headed goose.

The methods employed in this study were in most respects the same as those

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described by Black & Tenney (1980). Steady-state values of ventilation were measured in a whole-body plethysmograph. A steady state was assumed to be established 10–15 min after the plethysmograph had equilibrated with a new gas mixture if repeated measurements at 5–10 min intervals were consistent with each other. Awake, undisturbed animals were exposed to various levels of hypoxia achieved by adding N_2 to air, and the response was expressed as the percent increase in ventilation with hypoxia over the mean ventilation measured while the bird was breathing air before and after each hypoxic exposure. Arterial blood samples (0·7 ml) were drawn from catheters previously implanted either in the radial artery under local lidocaine anaesthesia in the pheasants, or in a branch of the femoral artery under halothane anaesthesia (1·5 % in O_2) in the rheas. Blood gases and pH were measured with Radiometer O_2 and CO_2 electrodes and PHM 71 Acid Base Analyzer. Following the ventilation studies, dissociation curves were determined with a standard mixing technique (Edwards & Martin, 1966), using whole blood freshly drawn from cardiac puncture. Saturated blood samples, equilibrated for 10 min with 3 % CO_2: 30 % O_2: 67 % N_2 in an IL 137 tonometer at 41 °C, and deoxygenated samples equilibrated with 3 % CO_2: 97 % N_2 were mixed in volumetric ratios to achieve known saturations. Their P_{O_2}, P_{CO_2} and pH were then promptly measured. Equilibrations with 8·2 % CO_2 with and without 30 % O_2 were also used to establish the Bohr factor. All values were then corrected to a pH of 7·5.

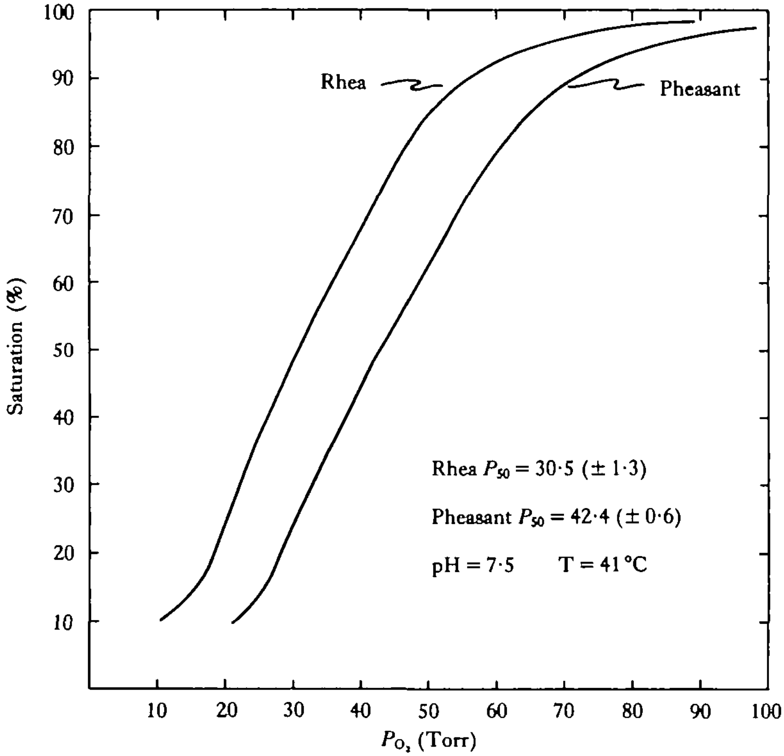

Fig. 1. Oxyhaemoglobin dissociation curves for the rhea and pheasant at pH = 7·5 and T = 41 °C. Rhea Hill coefficient (n) = 2·7; pheasant n = 3·4. Rhea Bohr factor = −0·61; pheasant Bohr factor = −0·35.

Table 1. *Average air-breathing respiratory characteristics*

	Tidal volume (ml BTPS)	Frequency (min^{-1})	Minute ventilation (ml BTPS min^{-1})
Rheas ($N = 2$)	55·7	9·67	537·5
Pheasants ($N = 3$)	8·4	35·8	307

Three young pheasants between 3·5 and 5 months of age (1·36, 1·02 and 0·99 kg), in adult plumage and of adult size, were used. Two young rheas, approximately 2–3 months old, but far from adult size, were also used in this study. One weighed 1·9 kg, the other weighed 2·2 kg. Preliminary studies of the ventilatory response to hypoxia were made on a total of four rheas including two smaller birds (0·59 kg and 0·42 kg),

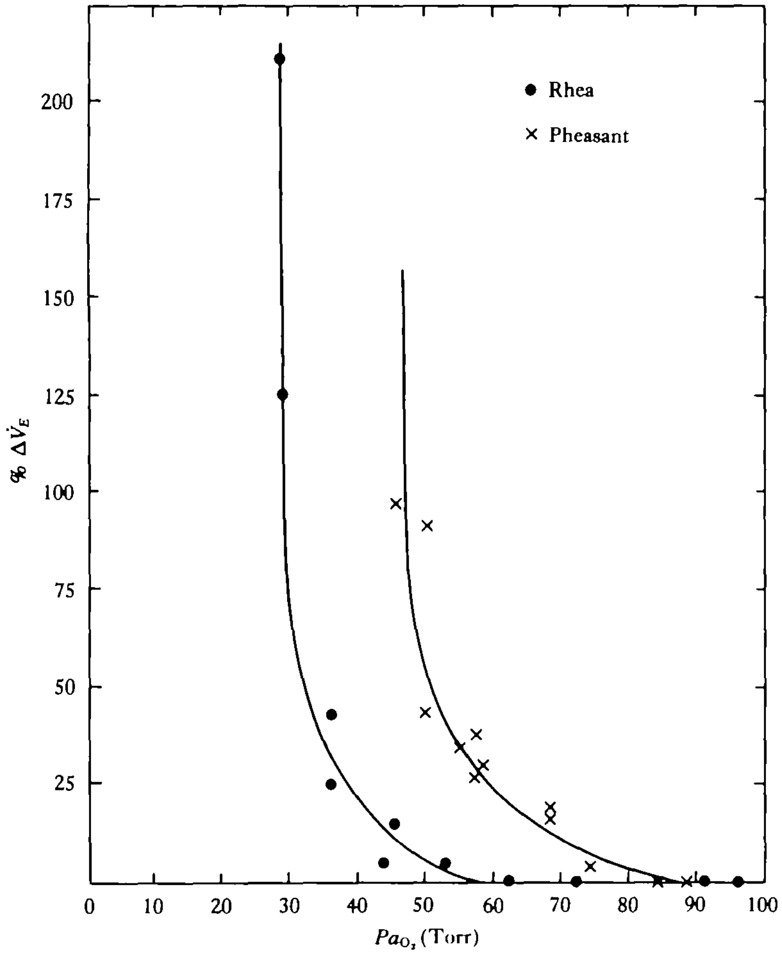

Fig. 2. Ventilatory response to hypoxia, expressed as the percent change from the normoxic ventilation (% $\Delta\dot{V}_E$). Points represent values from 3 pheasant (×) and 2 rheas (●).

but technical difficulties precluded use of the smaller ones in the blood gas/ventilation experiments reported here. Their ventilatory thresholds were the same as in the larger ones in their relationship to F_{IO_2} (fractional concentration of inspired O_2).

The 12 Torr difference in P_{50} between the rhea and pheasant presented in Fig. 1 is similar to the 14 Torr difference observed by Lutz *et al.* (1974). Our P_{50} values for these species are higher than those reported by Lutz *et al.* (1974) but the technique used by those investigators gives consistently lower values than all others (Baumann & Baumann, 1977). The pheasant P_{50} reported here is, however, essentially the same as the 42·2 reported by Isaacks *et al.* (1976) (corrected to 41 °C and pH = 7·5). The pheasant body temperature was in fact always 41 °C or higher, whereas the rhea body temperature was 39–40 °C. However, this small *in vivo* temperature difference would only have the effect of reducing the reported *in vitro* rhea P_{50} by 1–2 Torr, assuming the temperature coefficient of its haemoglobin is similar to that of other birds ($\Delta\log P_{50}/\Delta T = 0{\cdot}017\,°C^{-1}$, Baumann & Baumann, 1977).

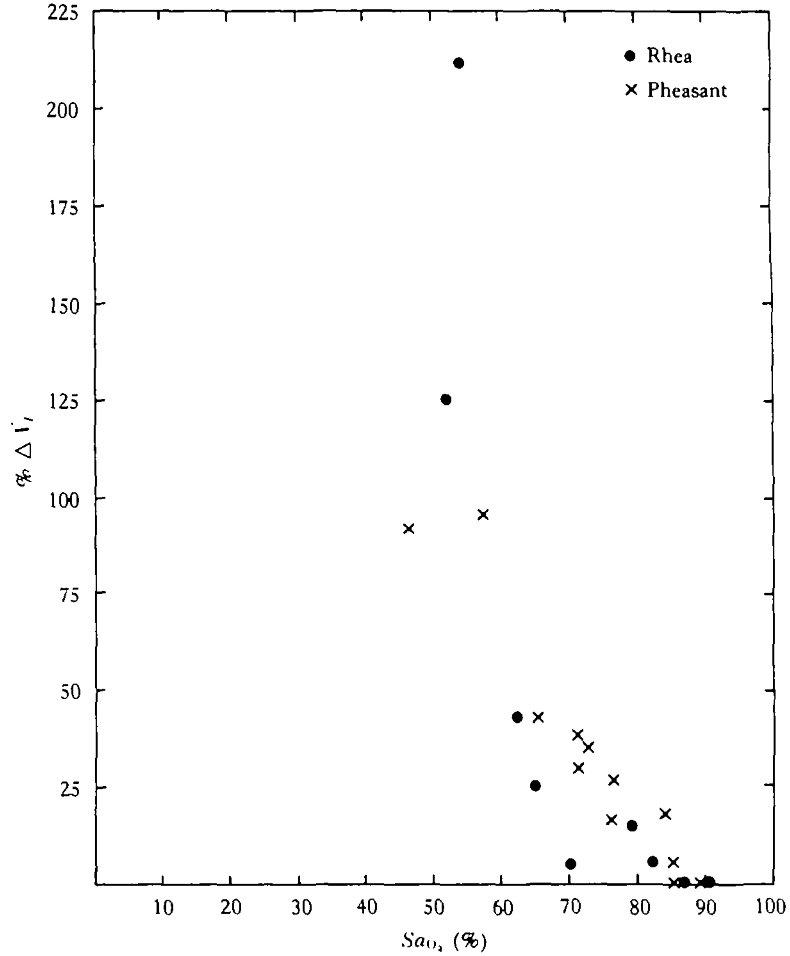

Fig. 3. Ventilatory response (% $\Delta\dot{V}_E$) to hypoxia plotted against arterial percent saturation (Sa_{O_2}) for rheas (●) and pheasants (×).

Resting respiratory pattern was different in the two species (Table 1). The rhea tidal volume (V_T) is larger and the pheasant V_T smaller than predicted on the basis of body weight (16·93 B.W.$^{1\cdot05}$, Bech, Johansen & Maloiey, 1979), while the rhea frequency (f) is less and pheasant frequency greater than predicted (17·2 B.W.$^{-0\cdot31}$, Lasiewski & Calder, 1971). The total minute ventilations, however, are within 5 % of the predicted values based on the product of the predicted V_T and *f*. The large tidal volume, low frequency pattern of the rhea appears to be typical of other birds with long necks, such as the mute swan (Bech & Johansen, 1980) and the flamingo (Bech *et al.* 1979). In both the pheasant and the rhea, the ventilatory response to hypoxia is due almost entirely to increases in respiratory frequency.

The first noticeable increase in ventilation in the rhea occurs at a Pa_{O_2} approximately 20 Torr below the Pa_{O_2} at which the pheasant begins to increase its ventilation (Fig. 2). There does appear to be a good correlation between that Pa_{O_2} at which ventilation begins to increase and the value of Pa_{O_2} at which the HbO_2 dissociation curve changes from the relatively flat upper portion to the more steeply sloped portions in each species. When the change in ventilation is plotted against Sa_{O_2} it can be seen that the increase in ventilation is initiated at approximately 80–85 % saturation (Fig. 3) in both species. Therefore the expectation of a correspondence in Pa_{O_2} between the 'knees' of the hypoxic ventilatory response curves and the 'knees' of the oxyhaemoglobin dissociation curves in two lowland avian species with differing haemoglobin O_2 affinities is borne out. For reasons already mentioned, that correspondence has important functional implications for the animals, but it need not imply anything fundamental about chemoreceptor function. It is most probably a consequence of natural selection favouring a high hypoxic ventilatory threshold in those species with a low affinity haemoglobin and a low threshold in those with a high oxygen affinity.

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