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AIR SAC GASES AND VENTILATION DURING PANTING IN FOWL, *GALLUS GALLUS*.

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Exposure to elevated environmental temperatures produces large increases in ventilation and respiratory evaporation in birds (Calder & Schmidt-Nielsen, 1967; Bouverot, Hildwein & LeGoff, 1974; Richards, 1976). Some workers have reported severe blood alkalosis in panting birds due to lung hyperventilation (Linsley & Burger, 1964; Calder & Schmidt-Nielsen, 1968; Frankel & Frascella, 1968), others only a small decrease in arterial P_{CO_2} (Marder, Arad & Gafni, 1974; Marder & Arad, 1975; Krausz, Bernstein & Marder, 1977). It has often been suggested, following Zeuthen (1942), that intrapulmonary valves may shunt air away from the parabronchi during panting thus alleviating the risk of hypocapnic alkalosis but such valves have not yet been demonstrated *in vivo*.

Recently Bech, Johansen & Maloiy (1979) showed that flamingoes, *Phoenicopterus ruber*, avoid hypocapnia during panting by restricting hyperventilation to the respiratory dead space. This is achieved by a 7-fold reduction of tidal volume, V_T to a value which closely matches the tracheal dead space, V_D. As a result of the diminished V_T, carbon dioxide accumulated within the respiratory system and rapid, shallow panting was periodically interrupted by bursts of 1–3 deeper breaths which served to flush out the excess carbon dioxide.

We have observed a similar pattern of respiration in domestic fowl *Gallus gallus* exposed for 1 h periods to environmental temperatures T_a of 35–40 °C. After 15–30 min of panting the mean P_{CO_2} of the interclavicular air sac fell by 3·5 torr whilst that of the abdominal air sac rose by 10·4 torr (Fig. 1). During each burst of deep respiration the gas composition of the abdominal sac transiently returned towards its resting, non-panting value and the measured rates of oxygen consumption $\dot{V}_{O_2}$ and carbon dioxide production $\dot{V}_{CO_2}$ transiently increased; at the same time end-tidal P_{O_2} fell markedly (Fig. 1, inset). These observations show that during shallow panting stale air accumulates within the caudal air sacs. This gas is used to ventilate the palaeopulmo during expiration but it is clear from the slight freshening of interclavicular sac gas, which is similar in composition to end-parabronchial gas, that gas exchange in the parabronchi is not impeded. This is also borne out by the slight fall in arterial P_{CO_2} (Table 1).

Recordings such as that in Fig 1, inset, do not give an accurate reflection of the composition of gas leaving the lung during shallow panting since the V_T is probably only slightly larger than the tracheal volume and the stale gas front fails to register

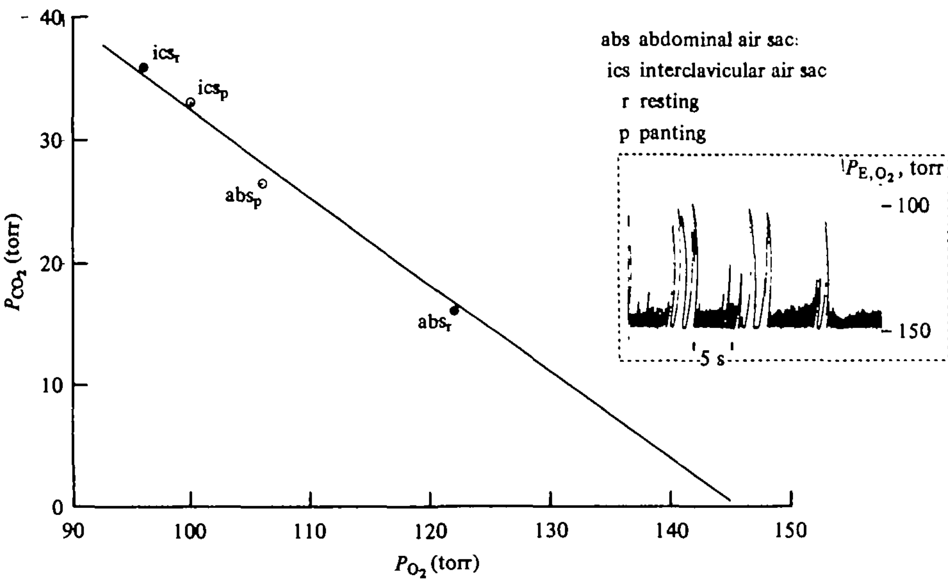

Fig. 1. P_{CO_2}–P_{O_2} diagram based on mean values for interclavicular and abdominal air sac gas composition during rest and panting. Inset shows recording of expired oxygen during panting. Air-sac gases were recorded continuously from permanently implanted cannulae. For the recording of expired oxygen the birds wore a tight-fitting mask connected to the atmosphere via a low-resistance breathing tube from which the gas sample was drawn.

Table 1. *Respiratory characteristics in awake chickens at rest and during panting*

(Data based on 12 animals. S.E. in parentheses. P_{a}, CO_2 and pH$_a$ measured in carotid artery. $\dot{V}_{O_2}$ measured by technique of Brackenbury & Avery (1980). V_D, From Kuhlmann & Fedde (1976). $\dot{V}$, $\dot{V}_l$ and $\dot{V}_D$ calculated according to method described in text).

	Rest	Panting	Rest/panting
W (kg)	2·2	—	—
T_a (°C)	18–22	35–40	—
T_b (°C)	41·51 (± 0·05)	42·83 (± 0·174)	—
P_a, CO_2, torr	26·2 (± 0·23)	24·8 (± 0·7)	—
pH$_a$	7·506 (± 0·006)	7·551 (± 0·012)	—
$\frac{\dot{V}_{O_2}}{W}$ $\left(\frac{\text{ml STPD}}{\text{kg-min}}\right)$	14·6 (± 0·76)	13·8 (± 0·87)	—
f (min^{-1})	15·4 (± 0·4)	174 (± 7·9)	11·3
V_D (ml BTPS)	8	8	—
$\dot{V}$ $\left(\frac{\text{ml BTPS}}{\text{kg-min}}\right)$	360	952	2·6
$\dot{V}_l$ $\left(\frac{\text{ml BTPS}}{\text{kg-min}}\right)$	304	319	1·05
$\dot{V}_D$ $\left(\frac{\text{ml BTPS}}{\text{kg-min}}\right)$	56	633	11·3
V_T (ml BTPS)	51·4	12·0	0·23

lly on the gas analyser. However, the P_{O_2} of end-expired gas during normal breathing and during sustained exercise is approximately 8 torr greater than that of interclavicular sac gas (J. Brackenbury, P. Avery & M. Gleeson, in preparation). Using interclavicular sac P_{O_2} as a gauge of end-expired gas it is possible to calculate the effective lung ventilation $\dot{V}_l$ from the measured $\dot{V}_{O_2}$ as follows: $\dot{V}_l = 876\ \dot{V}_{O_2}/(P_{IO_2} - P_{ics,O_2} - 8)$ ml BTPS min^{-1} where the figure 876 incorporates the factor for conversion from STPD to BTPS conditions. Dead space ventilation $\dot{V}_D$ was calculated from the measured respiratory frequency f multiplied by the dead space volume V_D.

Table 1 shows that despite a 2·6-fold increase in total ventilation $\dot{V}$, $\dot{V}_l$ increased by only 5% as a result of a 4-fold drop in V_T. The rise in the V_D/V_T ratio during panting automatically accounts for the observed increase in P_{CO_2} of the abdominal air sacs since, as Piiper (1978) has explained, the major source of CO_2 in the caudal air sacs is dead space gas re-inhaled from the trachea and primary bronchus at the beginning of each inspiration.

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