

SHORT COMMUNICATION

VENTILATORY OXYGEN EXTRACTION DURING COLD
EXPOSURE IN THE PIGEON (*COLUMBA LIVIA*)

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The respiratory responses to cold ambient temperatures in birds have only rarely been described. Bernstein & Schmidt-Nielsen (1974) studied the fish crow (*Corvus ossifragus*) during moderate cold exposure, while Bouverot, Hildwein & Oulhen (1976) measured ventilatory variables in pigeons (*Columba livia*) at near thermo-neutral (22°C) and at cold (2°C) ambient temperatures. With respect to the amount of oxygen extracted from the ventilated air, both studies did not show any significant alterations correlated with changes in ambient temperature. However, several recent studies have demonstrated an increased oxygen extraction (E_{O_2}) in response to cold exposure in birds [Bucher (1981) in the lined parakeet (*Bolborhynchos lineola*), Brent, Rasmussen, Bech & Martini (1983) in the kittiwake (*Rissa tridactyla*), Brent, Pedersen, Bech & Johansen (1984) in the European coot (*Fulica atra*) and Bech, Johansen, Brent & Nicol (1984) in the duck (*Anas platyrhynchos*)]. The significance of such an altered E_{O_2} is obvious: the resultant decrease in ventilatory requirement will lower the relative loss of heat and water. Thus, together with a low expired air temperature (Schmidt-Nielsen, Hainsworth & Murrish, 1970), the increased oxygen extraction serves to minimize the respiratory heat and water loss in cold environments (Johansen & Bech, 1983).

In most of the studies in which changed E_{O_2} values have been described, ventilatory volumes have been measured by pneumotachography (Brent *et al.* 1983, 1984; Bech *et al.* 1984). Thus, the birds were wearing a small face-mask and the ventilated air was forced through a Fleisch-tube (Glass, Wood & Johansen, 1978; Bech, Johansen & Maloiy, 1979). Recently, Barnas & Rautenberg (1984) used body plethysmography to measure the respiratory responses to cold in pigeons. Their results revealed a constant oxygen extraction with changed ambient temperature, thus confirming the results of Bouverot *et al.* (1976). Barnas & Rautenberg (1984) therefore questioned the results obtained in earlier studies using pneumotachography and claimed that 'differences in responses may, . . . , reflect differences in experimental methods rather than in species'.

Key words: Birds, cold exposure, ventilation, oxygen extraction.

To examine this question, we have used the pneumotachographic method to measure the respiratory variables, including oxygen extraction, in pigeons exposed to thermoneutral and cold ambient temperatures.

Two pigeons (body weights 339 and 533 g) were used in the study. For each individual a flexible face-mask was constructed from silicone-rubber. A Fleisch-tube was constructed from the barrel of a 1 ml syringe, in which smaller sections of PP 60 tubings were inserted. Total dead space of the mask was approximately 0.5 ml. Ventilation volumes were measured using a Could pneumotachograph (type 17212). For further details about the method see Glass *et al.* (1978) and Bech *et al.* (1979). Both specimens were equipped with spinal tubing according to Rautenberg, Necker & May (1972), allowing us to cool the vertebral canal in addition to environmental cooling. The oxygen consumption was measured with an open-flow system using a Servomex O₂-analyser.

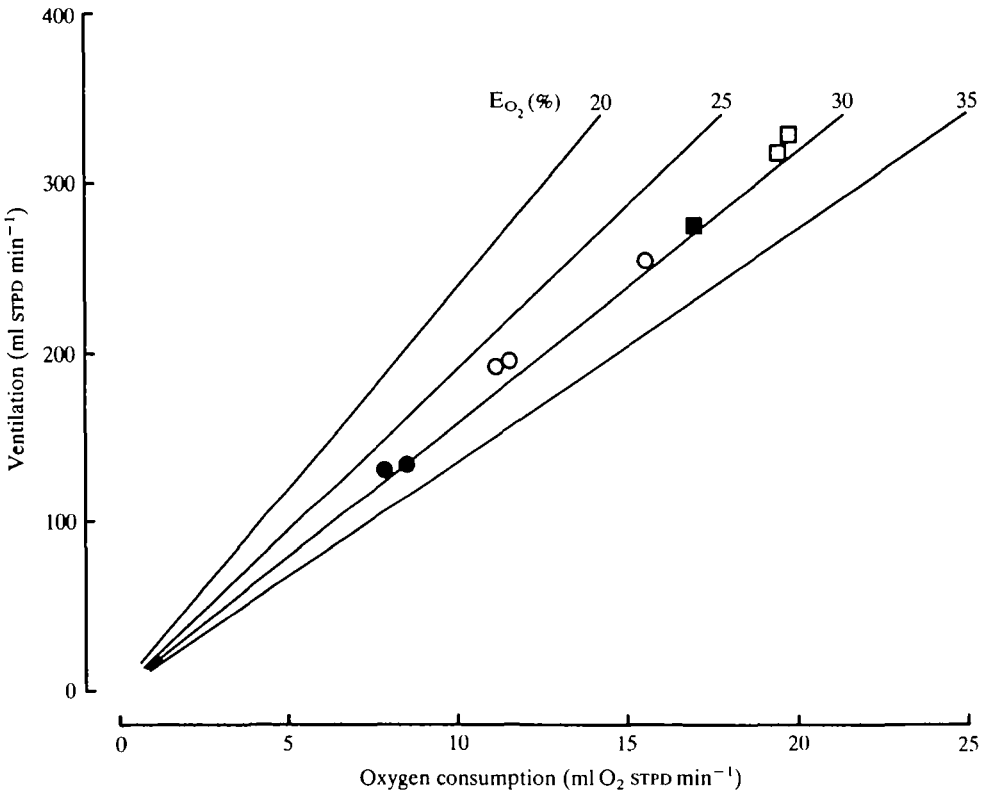


Fig. 1. Simultaneously obtained values of oxygen consumption and inspired ventilation in eight experiments including two specimens of *Columba livia*. E_{O_2} is calculated as $(\dot{V}_{O_2} \times 100) / (\dot{V}_I \times 0.2095)$, where \dot{V}_{O_2} is the oxygen consumption and \dot{V}_I is the inspired ventilation, both parameters expressed in STPD conditions. The diagonal lines mark equal oxygen extractions. Ambient temperature: (●) 25°C, (○) 5°C, (■) 25°C with spinal cooling, (□) 5°C with spinal cooling.

By combining environmental and spinal cooling we were able to induce various levels of oxygen consumption, the highest value corresponding to a heat production of 19.4 W kg^{-1} , which is about three times the basal value measured at 25°C (6.4 W kg^{-1}). Shivering can maximally increase the heat production by a factor of five in pigeons (Rautenberg, 1983), and the present experiments therefore cover most of the range of heat production possible during cold exposure.

The results show that the oxygen extraction did not change as a result of either cold exposure or combinations of cold and spinal cooling (Fig. 1). Thus, no matter how much the oxygen consumption was elevated above the thermoneutral level, ventilation increased in exactly the same proportion, thereby conserving the oxygen extraction and thus the ventilatory requirement. The mean oxygen extraction was 28.8% (S.D. = 0.8%, $N = 8$), and the ventilatory requirement was $0.372 \text{ litre mmol}^{-1}$ (S.D. = $0.01 \text{ litre mmol}^{-1}$, $N = 8$).

These results agree with those of Bouverot *et al.* (1976) and Barnas & Rautenberg (1984) in that E_{O_2} values do not change in response to cold exposure in pigeons. However, the absolute level of the oxygen extraction is somewhat higher than reported earlier in pigeons. Bouverot *et al.* (1976) and Barnas & Rautenberg (1984) found values of 23.1% and 19.7%, respectively, while the oxygen extraction in the present study was found to be 28.8%.

Mitchell & Osborne (1980) found that artificially increasing the respiratory dead space in chickens did not influence the respiratory frequency but caused an increased tidal volume, the increase being proportional to the increase in dead space. In the present study, the mask added an extra dead space of 0.5 ml, which is about 30% of the normal respiratory dead space in pigeons (Hinds & Calder, 1971). Adding 30% to the dead space in chickens enhanced the tidal volume by less than 15% (Mitchell & Osborne, 1980). Thus, we cannot disregard the possibility that using the mask, which imposes an increased respiratory dead space, could have slightly altered the respiratory pattern and therefore also the level of the oxygen extraction. However, this study has shown that employing pneumotachography does not necessarily induce artificial temperature-induced changes in oxygen extraction, and the claim advanced by Barnas & Rautenberg (1984) that the altered E_{O_2} found in some species of birds during cold exposure could be a result of the method used to measure it, seems therefore unjustified. Apparently there are species differences in the response to cold, with some species increasing the oxygen extraction, while others (e.g. pigeons) do not.

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REFERENCES

- BARNAS, G. & RAUTENBERG, W. (1984). Respiratory responses to shivering produced by external and central cooling in the pigeon. *Pflügers Arch. ges. Physiol.* **401**, 228–232.
- BECH, C., JOHANSEN, K., BRENT, R. & NICOL, S. (1984). Ventilatory and circulatory changes during cold exposure in the Pekin duck, *Anas platyrhynchos*. *Respir. Physiol.* **57**, 103–112.

- BECH, C., JOHANSEN, K. & MALOY, G. M. O. (1979). Ventilation and expired gas composition in the flamingo, *Phonicopterus ruber*, during normal respiration and panting. *Physiol. Zoöl.* **52**, 313–428.
- BERNSTEIN, M. H. & SCHMIDT-NIELSEN, K. (1974). Ventilation and oxygen extraction in the crow. *Respir. Physiol.* **21**, 393–401.
- BOUVEROT, P., HILDWEIN, G. & OULHEN, PH. (1976). Ventilatory and circulatory O₂ convection at 4000 m in pigeon at neutral and cold temperature. *Respir. Physiol.* **28**, 371–385.
- BRENT, R., PEDERSEN, P. F., BECH, C. & JOHANSEN, K. (1984). Lung ventilation and temperature regulation in the European coot, *Fulica atra*. *Physiol. Zoöl.* **57**, 19–25.
- BRENT, R., RASMUSSEN, J. G., BECH, C. & MARTINI, S. (1983). Temperature dependence of ventilation and O₂-extraction in the kittiwake, *Rissa tridactyla*. *Experientia* **39**, 1092–1093.
- BUCHER, T. L. (1981). Oxygen consumption, ventilation and respiratory heat loss in a parrot, *Bolborhynchus lineola*, in relation to ambient temperature. *J. comp. Physiol.* **142**, 479–488.
- GLASS, M., WOOD, S. & JOHANSEN, K. (1978). The application of pneumotrachography on small unrestrained animals. *Comp. Biochem. Physiol.* **59A**, 425–427.
- HINDS, D. S. & CALDER, W. A. (1971). Tracheal dead space in the respiration of birds. *Evolution* **25**, 429–440.
- JOHANSEN, K. & BECH, C. (1983). Heat conservation during cold exposure in birds (vasomotor and respiratory implications). *Polar Research* **1**, 259–268.
- MITCHELL, G. S. & OSBORNE, J. L. (1980). A comparison between carbon dioxide inhalation and increased dead space ventilation in chickens. *Respir. Physiol.* **40**, 227–239.
- RAUTENBERG, W. (1983). Thermoregulation. In *Physiology and Behaviour of the Pigeon*, (ed. M. Abs), pp. 131–148. New York: Academic Press.
- RAUTENBERG, W., NECKER, R. & MAY, B. (1972). Thermoregulatory responses of the pigeon to changes of the brain and the spinal cord temperatures. *Pflügers Arch. ges. Physiol.* **338**, 31–42.
- SCHMIDT-NIELSEN, K., HAINSWORTH, F. R. & MURRISH, D. E. (1970). Counter-current heat exchange in the respiratory passages: effect on water and heat balance. *Respir. Physiol.* **9**, 263–276.