EFFECTS OF COLD EXPOSURE ON OXYGEN CONSUMPTION, VENTILATION AND INTERCLAVICULAR AIR-SAC GASES IN THE LITTLE PENGUIN (*EUDYPTULA MINOR*)

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Summary

Oxygen consumption ($\dot{V}_{O_2}$), tidal volume, respiratory frequency and the composition of the gas in the interclavicular air sac were measured in the little penguin *Eudyptula minor* (Forster) at ambient temperatures (T_a) of 5 and 20°C.

$\dot{V}_{O_2}$ increased from $14.60\,\text{ml}\,O_2\,\text{kg}^{-1}\,\text{min}^{-1}$ at 20°C to $18.29\,\text{ml}\,O_2\,\text{kg}^{-1}\,\text{min}^{-1}$ at 5°C. However, the elevated $\dot{V}_{O_2}$ at the low T_a was not matched by a similar rise in total inspiratory ventilation ($\dot{V}_I$). The ventilatory requirement ($\dot{V}_I/\dot{V}_{O_2}$) thus decreased from $0.575\,l\,\text{mmol}^{-1}$ at 20°C to $0.440\,l\,\text{mmol}^{-1}$ at 5°C. An increased gas exchange efficiency during cold exposure was also shown by the composition of the gas in the interclavicular air sac. P_{O_2} decreased from 11.95 kPa at 20°C to 10.24 kPa at 5°C, while the corresponding increase in P_{CO_2} was from 6.61 to 7.50 kPa.

Oxygen extraction, calculated from $\dot{V}_{O_2}$, $\dot{V}_I$ and O_2 content of the inspired air, increased from 24.60 % at 20°C to 31.04 % at 5°C. Oxygen extraction calculated from the O_2 contents of inspired air and interclavicular air-sac gas was 38.73 % at 20°C and 47.18 % at 5°C.

The results confirm previous findings for the little penguin which showed a decrease in the ventilatory requirement with increasing oxygen uptake. However, the improved gas exchange efficiency during cold exposure and the strong correlation found between oxygen extraction and oxygen consumption have not been demonstrated previously for this species.

Introduction

It is well established that the avian respiratory system plays an important part in thermoregulation during heat stress, but the interaction between respiration and temperature control at low ambient temperatures is still not fully clarified

(Johansen and Bech, 1984; Barnas and Rautenberg, 1987). It has been proposed that an increase in the amount of oxygen extracted from the inspired air serves as a thermoregulatory mechanism under cold conditions (Bucher, 1981). An increased oxygen extraction by the lung will result in a lowering of the ventilatory requirement, thereby reducing the respiratory heat and water losses.

Simultaneous measurements of oxygen consumption and ventilation at ambient temperatures below the thermoneutral zone have only been made for a limited number of bird species. The results so far obtained show no general trend of a decrease in the ventilatory requirement in cold conditions. In some species, the increase in oxygen uptake associated with shivering is not accompanied by an equivalent increase in total inspiratory ventilation (Bucher, 1981; Brent *et al.* 1983, 1984; Bech *et al.* 1984). Thus, for these species the values of oxygen extraction calculated from oxygen consumption, total inspiratory ventilation and the fractional O_2 content in inspired air are higher during cold exposure. In other species, however, the increase in total inspiratory ventilation is well correlated with the increase in oxygen uptake induced by low ambient temperatures (Bernstein and Schmidt-Nielsen, 1974; Bech *et al.* 1985; Chappell and Bucher, 1987; Clemens, 1988).

A more direct way of estimating the gas exchange efficiency in birds is by making simultaneous measurements of the oxygen contents of the inspired air and the end-parabronchial gas, where the latter can be represented by the gas in one of the cranial air sacs (Powell *et al.* 1981). In ducks, *Anas platyrhynchos*, the only birds for which such measurements have been made at low ambient temperatures, the oxygen content of the interclavicular air sac decreases during cold exposure. The value of oxygen extraction calculated from the difference in O_2 content between inspired air and interclavicular air-sac gas is therefore elevated, indicating an increased oxygen extraction by the lung (Bech *et al.* 1984; Bech and Johannesen, 1989; Johannesen and Bech, 1989).

Stahel and Nicol (1988) have recently estimated the ventilatory requirement of little penguins *Eudyptula minor* exposed to ambient temperatures between −5 and +35°C. Their regression equation, describing the linear relationship between total inspiratory ventilation and oxygen consumption, indicates that for this species the ventilatory requirement decreased with increasing oxygen uptake. However, although the percentage of oxygen extracted from the total volume of air ventilated varied widely, from 37 to 72 %, no correlation existed between the oxygen extraction and the ambient temperature at temperatures ranging from −5 to +27°C. Above 25°C, oxygen extraction decreased with increasing ambient temperature.

In the present study of the little penguin, oxygen consumption, ventilation and the composition of the gas in the interclavicular air sac were measured simultaneously at both thermoneutral (20°C) and cold (5°C) ambient air temperatures. The objectives were to compare the two ways of determining oxygen extraction by the lung and to study the influence of changes in oxygen uptake and in ventilation on the gas exchange efficiency of this species.

Materials and methods

Four little penguins *Eudyptula minor*, caught at the time of completion of their moult in a nesting colony at Marion Bay, Tasmania, were used in the present study. The penguins were housed in an outdoor pen and fed every afternoon. A water supply was freely available. The investigation was made in March and April. Mean body mass during the experimental period was 892 ± 94 g ($\pm$s.D.). The penguins were released at the site of capture on completion of the experiments.

A catheter (Portex PP 160) was implanted, under Halothane anaesthesia, into the interclavicular air sac. The air-sac membrane was tied around the catheter, and the overlying muscles and skin were sutured tightly to prevent leaks. The catheter was then closed and taped to the skin. The penguins were allowed to recover for 2 days before the experiments started.

Measurements

On the days experiments were made, the penguins were placed in a cylindrical, double-walled, metabolic chamber (17 l). The air temperature (T_a) in the chamber was regulated at either 5 or 20°C by circulating a supply of thermostatically controlled brine through the outer annulus. For the little penguin it has been demonstrated that the thermoneutral zone extends from 10 to 30°C (Stahel and Nicol, 1982). A T_a of 5°C is therefore not very cold for this species, but in the present study the temperature in the chamber had to be kept above 0°C to avoid ice formation in the air-sac catheter. During the experiments, the air-sac catheter was elongated with flexible Tygon tubing, taped to feathers on the neck, and passed out of the chamber. Body temperature (T_b) was recorded by an Cr–Al thermocouple, inserted 5 cm into the cloaca and connected to an Impo Pt 200 microprocessor thermometer. The recordings were only made after at least 3 h of exposure to a constant T_a.

Metabolic and ventilatory parameters were determined simultaneously, in a positive-pressure, open-circuit system. The flow of dry air to the metabolic chamber was controlled by a Tylan FC 280 mass flow controller, calibrated against a spirometer. The outlet air was dried and samples were passed to the sample channel of a Servomex OA 184 oxygen analyzer and to a Beckman LB-2 carbon dioxide analyzer. Dry atmospheric air was simultaneously passed into the reference channel of the oxygen analyzer. The outputs from the gas analyzers were continuously recorded and also passed through an A/D converter to a computer, which calculated oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$), as described by Stahel and Nicol (1988).

Ventilatory parameters were determined by the barometric method. Changes in chamber pressure, due to the warming and humidification of inspired air, were measured using a Kyowa PG-10GC pressure transducer and recorded on a polygraph. Relative humidity in the chamber was measured with a Kane-May 8001 humidity sensor positioned at the air outlet. Mixing of the air contained in the chamber was achieved by using a small fan covered by a wire-mesh basket.

Chamber pressure was indicated by a water manometer and maintained at
0.78–0.98 kPa above the actual barometric pressure. The system was calibrated by
injecting a known volume of air, during the short period elapsing between two
successive breaths, at a rate that displayed the same slope of pressure signal as that
noted during inspiration. A series of 15–20 such calibration injections was made at
the end of each experiment, using a syringe connected to the chamber *via* a
three-way stopcock in the lid. Inspiratory tidal volume ($\dot{V}_T$) was calculated
according to equation 4 of Drorbaugh and Fenn (1955). Respiratory frequency (f)
was determined directly from the recorder chart.

When T_b, $\dot{V}_{O_2}$ and f were low and stable, gas samples were drawn from the air-
sac catheter by a 10 ml glass syringe at a rate of about 5 ml min^{-1}. The samples
were injected into the measuring cell of either a Beckman OM-11 oxygen analyzer
or a Beckman LB-2 carbon dioxide analyzer, *via* a tube containing 1.5 ml of
Beckman desiccant. The composition of the inspired air was assumed to be
identical with that of the air emerging from the outlet of the metabolic chamber.

Calculations

All recordings were analysed over consecutive periods of 10 min. The values for
oxygen consumption are expressed for STPD conditions, while the tidal volume and
total inspiratory ventilation ($\dot{V}_I = f \times V_T$) values are given according to BTPS. The
simultaneously measured O_2 and CO_2 contents in the air-sac gas were converted to
the equivalent partial pressures at the penguin's body temperature and the
prevailing barometric pressure. Gas exchange efficiency was calculated from the
following formulae:

$$E_{O_2} = 100(F_{IN_{O_2}} - F_{IC_{O_2}})/F_{IN_{O_2}}, \tag{1}$$

$$E'_{O_2} = (\dot{V}_{O_2} \times 100)/(\dot{V}_I \times F_{IN_{O_2}}), \tag{2}$$

where $F_{IN_{O_2}}$ and $F_{IC_{O_2}}$ are the fractional O_2 contents of the inspired air and of the
gas in the interclavicular air sac, respectively, $\dot{V}_{O_2}$ is oxygen consumption and $\dot{V}_I$ is
total inspiratory ventilation, after conversion of both values to STPD conditions.

Results

The results obtained for little penguins exposed to thermoneutral (20 °C) and to
cold (5 °C) ambient temperatures are shown in Table 1. Oxygen consumption
increased by 25 % when T_a was lowered from 20 to 5 °C. However, the increase in
$\dot{V}_{O_2}$ during cold exposure was not accompanied by an equivalent rise in total
inspiratory ventilation. Both tidal volume and respiratory frequency remained
unchanged. There was consequently no change in the effective ventilation, and the
simultaneous decrease in the gas exchange ratio (RE) indicates that there was
hypoventilation. This resulted in a significant reduction in the ventilatory
requirement ($\dot{V}_I/\dot{V}_{O_2}$), which decreased from 0.5751 mmol^{-1} at 20 °C to
0.4401 mmol^{-1} at 5 °C. The amount of oxygen extracted from the total volume of

Table 1. *Gas exchange variables in the little penguin at two ambient temperatures*

	20°C (N=31)		5°C (N=23)		
	Mean	2 S.E.M.	Mean	2 S.E.M.	P*
$\dot{V}_{O_2}$ (ml O_2 STPD $kg^{-1} min^{-1}$)	14.60	0.59	18.29	0.35	<0.001
$\dot{V}_{CO_2}$ (ml CO_2 STPD $kg^{-1} min^{-1}$)	11.37	0.30	13.35	0.31	<0.001
RE	0.78	0.02	0.73	0.02	<0.001
$\dot{V}_T$ (ml BTPS kg^{-1})	36.02	2.33	35.58	1.58	NS
f (min^{-1})	10.2	0.3	10.1	0.5	NS
$\dot{V}_I$ (ml BTPS $kg^{-1} min^{-1}$)	365.20	20.38	360.18	26.03	NS
$\dot{V}_I/\dot{V}_{O_2}$ (l BTPS $mmol^{-1}$)	0.575	0.052	0.440	0.027	<0.001
$P_{IC_{O_2}}$ (kPa)	11.95	0.47	10.24	0.36	<0.001
$P_{IC_{CO_2}}$ (kPa)	6.61	0.33	7.50	0.23	<0.001
E'_{O_2} (%)	24.60	2.14	31.04	1.92	<0.001
E_{O_2} (%)	38.73	2.34	47.18	1.80	<0.001

N, number of experiments; see text for explanation of other abbreviations.
* Student's *t*-test; NS, not significant.

air ventilated (E'_{O_2}) increased simultaneously by 26 % compared to the value noted at 20°C.

The composition of the gas in the interclavicular air sac changed markedly in response to cold exposure (Table 1). P_{O_2} in the interclavicular air-sac gas was lower at 5°C than at 20°C (by 1.71 kPa on average), while P_{CO_2} was higher (by 0.89 kPa on average). The substantial decrease in the fractional O_2 content of the gas in the interclavicular air sac at the low T_a (from 0.126 to 0.109) resulted in a 22 % elevation of the oxygen extraction calculated from the O_2 contents of inspired air and interclavicular air-sac gas (E_{O_2}).

The observed increase in E'_{O_2} under cold conditions was almost exclusively the result of an increase in oxygen consumption, since the mean total inspiratory ventilation remained constant. The increase in E_{O_2} was due to a reduction in the oxygen content of the gas in the interclavicular air sac. Fig. 1 shows that a strong relationship existed between oxygen extraction (both E'_{O_2} and E_{O_2}) and oxygen consumption. The changes in tidal volume and in respiratory frequency, however, were not correlated with changes in either E'_{O_2} or E_{O_2}.

Discussion

The thermoneutral zone for the little penguin extends from 10 to 30°C (Stahel and Nicol, 1982). The mean $\dot{V}_{O_2}$ that we measured within the thermoneutral zone, at 20°C, is equivalent to a metabolic heat production of 4.89 W kg^{-1}. This value is in close agreement with the basal metabolic rate of 4.93 W kg^{-1} reported by Stahel and Nicol (1982), but is substantially higher than the minimum value of 3.3 W kg^{-1} found in a more recent study (Stahel and Nicol, 1988). A seasonal variation in the standard metabolic rate may account in part for this difference. The penguins used
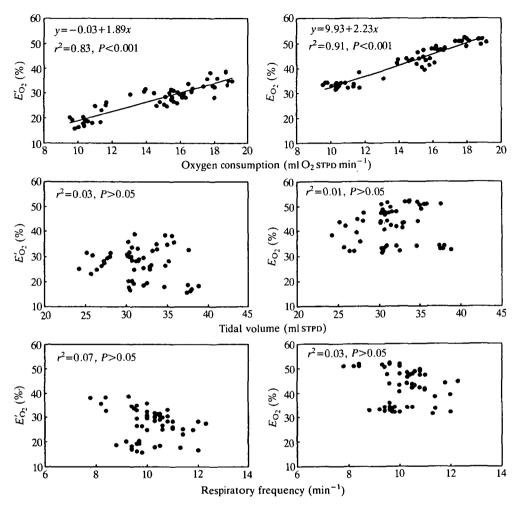
Fig. 1. On the left: oxygen extraction (E'_{O_2}) calculated from oxygen consumption, total inspiratory ventilation and the fractional oxygen content of the inspired air plotted as a function of oxygen consumption, tidal volume and respiratory frequency. On the right: oxygen extraction E_{O_2} calculated from the fractional oxygen contents of inspired air and interclavicular air-sac gas plotted as a function of oxygen consumption, tidal volume and respiratory frequency. For definitions of E'_{O_2} and E_{O_2} see equations 1 and 2 in the text.

in the current study had just completed their annual moult, and the experiments were made at the same time of year as the first investigation by Stahel and Nicol (1982). It is also obvious that body mass has a strong influence on the mass-specific metabolic rate. The mean body mass of our penguins was the same as that of those used in the first study by Stahel and Nicol (1982), but was significantly lower than the mean body mass (1082 g) reported in their later study (Stahel and Nicol, 1988). It is also worth noting that, in the present study, the experiments were made within a month of capture, whereas most of the penguins used in the later study by Stahel

and Nicol (1988) had been kept in captivity for more than a year prior to the experiments and were used to being handled.

At 20°C, both the mean respiratory frequency (10.2 min^{-1}) and the mean tidal volume (30.9 ml) were higher than the minimum values given by Stahel and Nicol (1988), where a mean f of 6.9 min^{-1} was measured at T_a values between 15 and 20°C and a mean $\dot{V}_T$ of 14.9 ml was measured at T_a values between 10 and 15°C. However, these mean values were based on a relatively small number of measurements (nine and four, respectively), and they represent minimum values within 5°C T_a ranges rather than average values within the entire thermoneutral zone. The differences found in the ventilatory parameters are therefore not so dramatic and may be explained by the difference in ambient temperature. According to Bucher (1985), ventilatory parameters in birds can change within, as well as below and above, the thermoneutral zone. Identical equipment was used in both studies, except that the metabolic chamber used by Stahel and Nicol (1988) was larger (25 l). Even though our penguins had a higher oxygen consumption than those studied by Stahel and Nicol (1988), this alone cannot explain the higher total ventilation. Oxygen extraction, calculated from oxygen consumption and total inspiratory ventilation measured at thermoneutrality, is therefore substantially lower than the mean value of 54.5 % reported by Stahel and Nicol (1988).

Although the study of Stahel and Nicol (1988) revealed no clear correlation between E'_{O_2} and T_a, in the present study both E'_{O_2} and E_{O_2} increased significantly when T_a was lowered from 20 to 5°C. The variation in E'_{O_2} at a given T_a was also substantially smaller than that found by Stahel and Nicol (1988). Bucher (1981) found that parrots, *Bolborhynchus lineola*, responded to even minor disturbances by increasing their respiratory frequency and oxygen consumption and by decreasing their oxygen extraction. This pattern was also observed in the present study on the little penguin. Quite minor disturbances resulted in higher f, $\dot{V}_{O_2}$ and $P_{IC_{O_2}}$ values, resulting in E'_{O_2} and E_{O_2} values substantially below the regression lines shown in Fig. 1. These data have not been included in the present results. Respiratory frequency and oxygen consumption are therefore very labile and any type of disturbance or restraint can easily mask the normal responses to changes in ambient temperature. The inclusion of data from even lightly stressed birds may explain some of the discrepancies, regarding the relationship between E'_{O_2} and T_a, between our findings in this study and those of Stahel and Nicol (1988).

The only other data on air-sac gases in penguins are those of Powell and Hempleman (1985) for two gentoo penguins *Pygoscelis papua* and one chinstrap penguin *Pygoscelis antarctica*, both of which were anaesthetized and artificially ventilated. The mean $P_{IC_{O_2}}$ and $P_{IC_{CO_2}}$ values for these two species were 15.7 kPa and 3.0 kPa, respectively. For the little penguin, $P_{IC_{O_2}}$ measured at thermoneutrality (11.95 kPa) was significantly lower and the corresponding $P_{IC_{CO_2}}$ (6.61 kPa) significantly higher. This difference could be attributed to more efficient gas exchange of the little penguin compared to that of the other two penguin species investigated. However, in a study on the domestic fowl *Gallus gallus* Piiper *et al.* (1970) found that $P_{IC_{O_2}}$ was substantially lower in spontaneously breathing birds

than in birds that were artificially ventilated. It is also worth noting that the composition of the gas in the interclavicular air sac of our penguins, at thermoneutrality, was similar to the values reported by Stahel and Nicol (1988) for the end-expired air in the same species.

The decrease in ventilatory requirement observed when T_a was lowered from 20 to 5°C could, in theory, be achieved by two quite different mechanisms. There could be either an alteration in the ventilatory pattern, so that a smaller portion of the total ventilation is dead space ventilation, or an increase in the gas exchange efficiency of the parabronchial lung itself. Our data indicate that no relationship existed between oxygen extraction and the ventilatory parameters. It is therefore tempting to assume that, in the little penguin, the decrease in the ventilatory requirement at a T_a of 5°C is exclusively the result of an increase in lung efficiency. This conclusion contrasts with the findings made for the kittiwake *Rissa tridactyla* (Brent *et al.* 1983), the Pekin duck (Bech *et al.* 1984) and the European coot *Fulica atra* (Brent *et al.* 1984). In all these species, an alteration in the ventilatory pattern, involving higher $\dot{V}_T$ and constant or reduced f, is observed. It is not surprising, however, that our observed E_{O_2} values were higher than the corresponding E'_{O_2} values. The latter is a measure of the percentage of oxygen taken up from the amount available in the total volume of air ventilated, whereas the parabronchial ventilation, i.e. the ventilation of the gas exchange region, is equal to the total ventilation minus the dead-space ventilation (Scheid and Piiper, 1987). To calculate correct values for lung efficiency from measurements of oxygen consumption and ventilation, the ventilation of the gas exchange region must also be known.

A strong correlation between oxygen extraction and oxygen consumption (Fig. 1) has also been demonstrated for ducks, for which the rise in oxygen extraction during cold exposure is more a response to an increase in oxygen uptake than an effect of the lower ambient temperature *per se* (Bech and Johannesen, 1989).

The thermoregulatory benefit of an increase in lung efficiency during cold exposure is a matter of debate and the existing data are limited. However, a decrease in the ventilatory requirement at low ambient temperature does result in lower respiratory heat and water losses. The most complete data exist for the European coot (Brent *et al.* 1984). For this species, the energy cost of heating dry, inspired air to body temperature amounted to 24 % of the total metabolic heat production at a T_a of −25°C. The energy cost due to water vapour saturation of the inspired air was not estimated. 79 % of the energy used to warm up the inspired air at an ambient temperature of −25°C was recovered by subsequent cooling of the expired air to nearly 0°C, while a further 11 % saving was achieved by a reduction in the ventilatory requirement (Brent *et al.* 1984). Although the latter value corresponds to only 2.6 % of the total metabolic heat production at −25°C, and thus might seem to be of only limited significance, the heat recovered represents more than 50 % of what would have been lost if oxygen extraction were to have remained constant during the cold exposure. Because only a limited

number of bird species have been carefully studied, the question of the importance of interspecific differences cannot be resolved at present.

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