

VENTILATION AND GAS EXCHANGE DURING SHALLOW HYPOTHERMIA IN PIGEONS

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Summary

Ventilatory control of the composition of the gases in the air sacs was studied during entry into fasting-induced, shallow, nocturnal hypothermia in the domestic pigeon (*Columba livia*). Respiratory frequency (f), tidal volume (V_T) and oxygen uptake (\dot{V}_{O_2}) were recorded simultaneously in six pigeons; partial pressures of CO_2 and O_2 in the abdominal and interclavicular air sacs were measured in seven pigeons. Ambient temperature was 25°C (thermoneutral) and the body temperature (T_b) was recorded in all experiments.

A reduction in T_b from 40.5 to 37.5°C paralleled decreases in f and V_T from 13.3 min^{-1} and 15.2 ml BTPS kg^{-1} to 10.7 min^{-1} and 12.4 ml BTPS kg^{-1} , respectively. There was a minor, but non-significant, simultaneous decrease in the ventilatory requirement (total ventilation/ O_2 uptake) from 0.38 to 0.35 ml BTPS mmol^{-1} . However, in both air sacs the partial pressure of CO_2 increased when T_b decreased, indicating an effective parabronchial hypoventilation.

The results support the idea of a gradually developing respiratory acidosis during hypothermia.

Introduction

There is a growing body of evidence that animals entering periods of torpor develop a respiratory acidosis. This may be important as a means of inhibiting cell metabolism (Malan, 1980, 1986). Even though such an acidosis has been demonstrated in widely different species of animals (Malan, 1980; Barnhart, 1989), this aspect of hypothermia has not been investigated in birds. In a parallel paper (Jensen and Bech, 1992), we have described the arterial acid–base balance of the domestic pigeon (*Columba livia*) during shallow nocturnal hypothermia and have shown that respiratory acidosis does indeed develop in this species simultaneously with a reduction in body temperature and oxygen consumption.

As the short-term regulation of systemic pH is mainly accomplished by adjusting the ratio of ventilation to CO_2 production, it was of interest to analyze the ventilatory changes that take place during regulated hypothermia. In previous papers on ventilation in torpid birds no clear-cut conclusions could be drawn

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regarding the acid–base changes (Withers, 1977a; Bucher and Chappell, 1989). Thus, the aim of the present study was to quantify the ventilatory changes and the changes in the composition of the air-sac gases during entry into shallow nocturnal hypothermia in the pigeon, paying special attention to the regulation of the arterial partial pressure of CO₂.

In mammals, entry into torpor is accompanied by an early and sudden decrease in the gas exchange ratio, indicating an early build-up of CO₂ and a lowering of the pH of the blood (Bickler, 1984; Nestler, 1990). In snails entering estivation, a decrease in the respiratory gas exchange ratio has been found concomitant with decreases in pH and in oxygen consumption (Rees and Hand, 1990). Furthermore, during the initial stage of arousal from hibernation, the European hamster (*Cricetus cricetus*) has been shown to hyperventilate, releasing CO₂ and increasing its blood pH before thermogenesis is fully activated (Malan *et al.* 1988).

By measuring the arterial pH and partial pressure of CO₂ in the pigeon, we were unable to demonstrate such an early build-up of CO₂. Acidosis seemed to develop gradually, i.e. there was a constant pH *in vivo* during entry into hypothermia. Consequently, another aim of the present study was to investigate whether the changes in the ventilatory variables were consistent with such a gradual development of acidosis.

Materials and methods

Experimental birds and procedures

Before the start of the experiments, domestic pigeons of both sexes were deprived of food for 1–2 weeks, with water available *ad libitum*. Thus, when the experiments were carried out, the pigeons were in phase II (Cherel *et al.* 1988) of their fasting period. They were kept in cages at room temperature (20±2°C) with a constant photoperiod, 10 h:14 h L:D. This photoperiod was maintained during the experiments, but the experimental ambient temperature (T_a) was 25±1°C (thermoneutral). Recordings were started in the light phase at 15:00–16:00 h after a 1 h stabilization period; the light was turned off at 17:00 h and recording continued during the entry into hypothermia, until about 23:00 h.

Two different experimental protocols were used. In six pigeons, rate of oxygen consumption (\dot{V}_{O_2}), respiratory frequency (f) and inspired tidal volume (V_T) were measured simultaneously. In seven other pigeons, the partial pressures of CO₂ and O₂ in the interclavicular and abdominal air sacs were measured. The mean body masses of the two groups of pigeons before the fasting period were 467 g (range 401–530 g) and 511 g (range 476–552 g), respectively. During the experiments the mean body masses were 337 g (range 293–400 g) and 376 g (range 335–418 g), respectively. Body temperature (T_b) was measured in all the experiments.

Body temperature and rate of oxygen consumption

\dot{V}_{O_2} and T_b were measured as described by Jensen and Bech (1992). Briefly, air was sucked through a 7 l metabolic chamber and the effluent air directed into an

oxygen analyzer (type 1100A, Servomex, England) for continuous recording of the O_2 content. \dot{V}_{O_2} was calculated according to Withers (1977b), assuming a respiratory gas exchange ratio of 0.75. T_b was measured with a copper-constantan thermocouple (type 0.005, Finewire, California), inserted into a blind-ending tube (PP 30) implanted into the peritoneal cavity.

The state during which T_b was above $40.0^\circ C$ will be referred to as euthermia. When referring to hypothermia, the T_b range will be defined in each case.

Values of \dot{V}_{O_2} are expressed as $ml\ STPD\ kg^{-1}\ min^{-1}$.

Ventilation

The pigeons were placed in a metabolic chamber during the experiments, so that \dot{V}_{O_2} could be measured simultaneously with the ventilatory variables. Pneumotachography was used to measure V_T and f (Glass *et al.* 1978). Each pigeon was fitted with a mask that covered its beak and nostrils and from which a 4 cm long tube protruded (Fleisch flow transducer head). Flexible tubing attached to the head of the flow transducer was led out of the chamber and connected to a Godart pneumotachograph (Gould Inc., type 17212). Before starting each experiment, calibrations were made by injecting known volumes of air through the head of the flow transducer using a plastic syringe.

The rate of inspired ventilation (\dot{V}_I) was calculated according to equation 1:

$$\dot{V}_I = fV_T \quad (1)$$

and the values are expressed as $ml\ BTPS\ kg^{-1}\ min^{-1}$. \dot{V}_{O_2} was converted to $mmol\ kg^{-1}\ min^{-1}$ ($1\ mmol\ O_2 = 22.414\ ml\ O_2$) before the ventilatory requirement (\dot{V}_I/\dot{V}_{O_2}) was calculated. The tracheal dead space (V_D) was calculated according to Hinds and Calder (1971) and the values were used to calculate the effective parabronchial ventilatory requirement (\dot{V}_P/\dot{V}_{O_2}) according to the equation:

$$\dot{V}_P/\dot{V}_{O_2} = f(V_T - V_D)/\dot{V}_{O_2}, \quad (2)$$

where \dot{V}_P is the rate of parabronchial ventilation.

Air-sac gases

Each pigeon was fitted, under halothane anesthesia, with two polypropylene tubes (PP 120), one inserted into the interclavicular air sac and the other into the right abdominal air sac. The tubes were firmly fixed to the surrounding muscles and skin with surgical thread. The tubes were sealed and the pigeons were allowed at least 2 days in which to recover before any air samples were taken.

During an experiment the pigeon was placed in the metabolic chamber for measurement of \dot{V}_{O_2} (see above). The two air-sac tubes were directed through an air-tight hole in the chamber wall and connected to a suction pump for sampling at a constant rate of $1\ ml\ min^{-1}$. 10–15 ml of air was sucked into air-tight plastic syringes for each sample.

The partial pressures of CO_2 and O_2 in the interclavicular air-sac samples (P_{ICCO_2} and P_{ICO_2}) and in the abdominal air-sac samples (P_{ABCO_2} and P_{ABO_2}) were

measured, at 40.0°C, on a blood gas analyzer (Radiometer, Denmark, type BMS 3 Mk 2 blood micro system). Before each experiment, the blood gas electrodes were calibrated, using two separate gas mixtures (2.96% CO₂/17.21% O₂/79.83% N₂ and 10.00% CO₂/9.97% O₂/80.03% N₂). The partial pressure of a gas in the air sac at body temperature was calculated assuming that the air-sac gas was saturated with water vapor.

The 'gas exchange ratio' for each air sac (RE) was calculated from the fractional concentrations (F) in the inspired air (I) and the air-sac gas (A), assuming that $F_{N_2} = 1 - F_{CO_2} - F_{O_2}$:

$$RE = (F_{ACO_2} - F_{ICO_2}) / (F_{IO_2} \times F_{AN_2} / F_{IN_2} - F_{AO_2}). \quad (3)$$

Evaluation and statistics

For overall mean values, the mean value for each individual pigeon was counted as a single observation. Results are expressed as means \pm 1 s.d. When testing for differences between mean values, a two-tailed paired-sample t -test was used.

Regression lines were calculated using the method of least squares. To determine whether the slope of the regression line differed significantly from zero, a two-tailed t -test was carried out. The chosen level of significance was $P < 0.05$.

Results

Individual recordings of \dot{V}_I/\dot{V}_{O_2} and \dot{V}_P/\dot{V}_{O_2} are shown in Fig. 1; the corresponding overall mean values from two T_b ranges are given in Table 1 along with the values of f , V_T , \dot{V}_I and \dot{V}_{O_2} . \dot{V}_I declined significantly during the entry into hypothermia; this was a consequence of reductions in both f and V_T . The

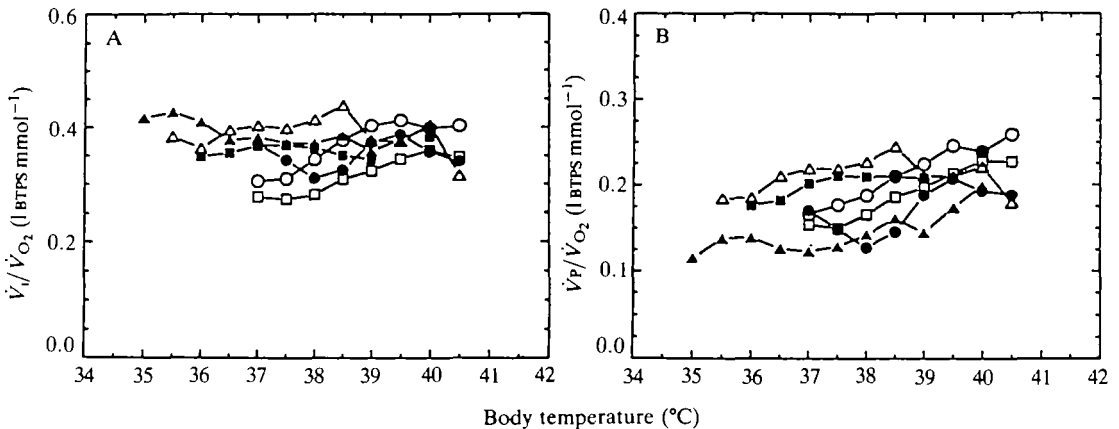


Fig. 1. Ventilatory requirement (\dot{V}_I/\dot{V}_{O_2}) (A) and effective parabronchial ventilatory requirement (\dot{V}_P/\dot{V}_{O_2}) (B) for six pigeons. Each point shows the mean value recorded for a 0.5°C change in body temperature.

Table 1. Mean respiratory variables (\pm s.d.) for two separate body temperature ranges

	40.0–41.0°C	P	37.0–38.0°C
f (min^{-1})	13.3 \pm 1.3	<0.01	10.7 \pm 1.2
V_T (ml BTPS kg^{-1})	15.2 \pm 1.5	<0.01	12.4 \pm 1.4
\dot{V}_I (ml BTPS $\text{kg}^{-1} \text{min}^{-1}$)	202.9 \pm 27.4	<0.01	132.8 \pm 10.3
\dot{V}_{O_2} (ml STPD $\text{kg}^{-1} \text{min}^{-1}$)	11.95 \pm 0.99	<0.001	8.69 \pm 1.17
\dot{V}_I/\dot{V}_{O_2} (ml BTPS mmol^{-1})	0.380 \pm 0.038	NS	0.346 \pm 0.045
\dot{V}_P/\dot{V}_{O_2} (l BTPS mmol^{-1})	0.225 \pm 0.030	0.05	0.170 \pm 0.031

The overall mean values were calculated from the individual means for six pigeons each used in experiments for one or two days.

The significance level shown is for the difference between the overall mean values; NS, not significant.

f , respiratory frequency; V_T , inspired tidal volume; \dot{V}_I , rate of inspired ventilation; \dot{V}_{O_2} , rate of oxygen consumption; \dot{V}_P , rate of parabronchial ventilation.

percentage declines in \dot{V}_I and \dot{V}_{O_2} were almost equal, so that even though some of the individual measurements showed a reduction in the \dot{V}_I/\dot{V}_{O_2} ratio when T_b decreased, the overall mean values for the lower and higher T_b ranges were not significantly different. However, the \dot{V}_P/\dot{V}_{O_2} ratio decreased significantly; on average by 24 % from euthermia to the T_b range 37–38°C.

Fig. 2 shows the partial pressures of the interclavicular and abdominal air-sac gases. From three pigeons, we obtained air samples from both air sacs simultaneously; in another two pigeons only the interclavicular air sac was sampled, and in two more pigeons only the abdominal air sac was sampled. All the data were used to calculate the overall mean values at euthermia and hypothermia

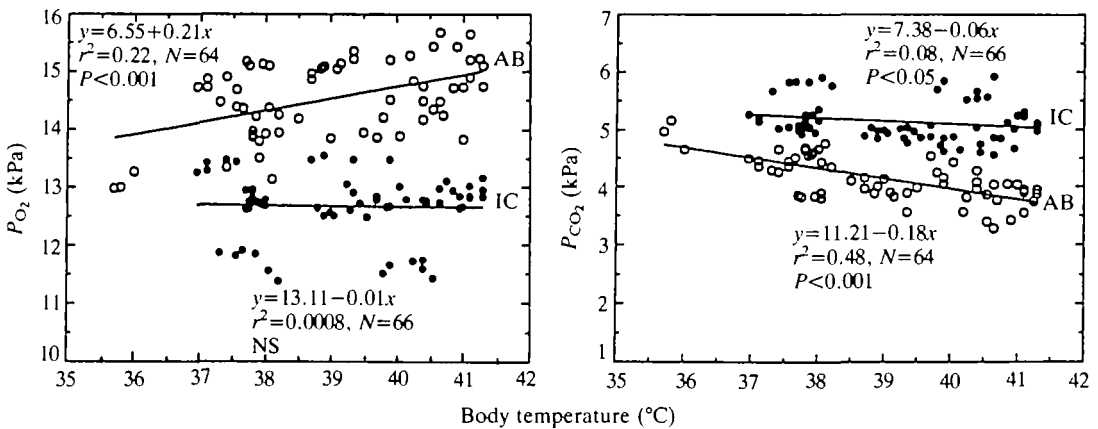


Fig. 2. Partial pressures of O_2 and CO_2 in the interclavicular (IC, filled circles) and abdominal (AB, open circles) air sacs, during the entry into hypothermia (recordings from five pigeons for each air sac). The mean barometric pressure was 99.1 \pm 1.5 kPa.

Table 2. Partial pressures of CO_2 and O_2 in the interclavicular air sac (P_{ICCO_2} and P_{ICO_2}) and the abdominal air sac (P_{ABCO_2} and P_{ABO_2}) during euthermia ($T_b=40.0-41.5^\circ C$) and hypothermia ($T_b=37.0-38.0^\circ C$)

T_b ($^\circ C$)	P_{ICCO_2} (kPa)	P_{ICO_2} (kPa)	P_{ABCO_2} (kPa)	P_{ABO_2} (kPa)
40.0-41.5	5.07 ± 0.36	12.62 ± 0.56	3.82 ± 0.25	14.79 ± 0.59
	$P < 0.05$	NS	$P < 0.001$	$P < 0.01$
37.0-38.0	5.25 ± 0.32	12.71 ± 0.56	4.38 ± 0.33	14.32 ± 0.68

Values are the overall means \pm s.d. for five pigeons each measured 2-4 times at each temperature interval.

The mean barometric pressure was 99.1 ± 1.5 kPa.

The significance levels for the differences between the means are indicated; NS, not significant.

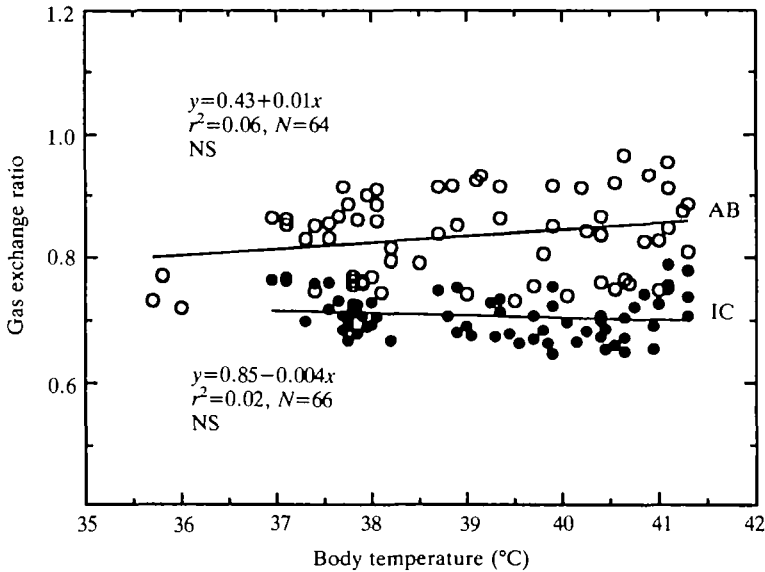


Fig. 3. The gas exchange ratio for the interclavicular (IC, filled circles) and abdominal (AB, open circles) air sacs of five pigeons, during entry into hypothermia.

($T_b=37.0-38.0^\circ C$) given in Table 2. The changes in the partial pressures of the air-sac gases were greater in the abdominal than in the interclavicular air sac. In the latter, only the partial pressure of CO_2 changed significantly. The changes in P_{ICCO_2} and P_{ABCO_2} were significantly different (different slopes, $P < 0.01$).

The gas exchange ratios (RE) of the air sacs, which are shown in Fig. 3, were not affected by the changes in T_b , but RE was considerably higher in the abdominal than in the interclavicular air sac.

Discussion

Ventilation

The respiratory frequency of birds has been found to increase as a result of using the pneumotachographic method of measurement (Bucher, 1985). Thus, the extra dead space imposed by the mask might have altered the normal respiratory variables for our pigeons. Stahel and Nicol (1988) found an increase in both f and V_T when the pneumotachographic method was used on the little penguin (*Eudyptula minor*) as compared to a barometric method. However, these same authors reported that the ventilation of ducks was not affected by the method used. Bech *et al.* (1985) measured the oxygen extraction of pigeons, in relation to the ambient temperature, using the pneumotachographic method. They concluded that oxygen extraction did not change in response to low ambient temperatures, the same conclusion as had previously been obtained using whole-body plethysmography (Barnas and Rautenberg, 1984), even though the absolute level of oxygen extraction was increased by wearing a mask. The value of \dot{V}_I/\dot{V}_{O_2} measured here ($0.380 \text{ l BTPS mmol}^{-1}$) does not differ significantly from that of $0.372 \text{ l BTPS mmol}^{-1}$ reported by Bech *et al.* (1985) for pigeons that had been fed. It should also be noted that the \dot{V}_{O_2} values measured in pigeons fitted with a mask ($11.95 \pm 0.99 \text{ ml STPD kg}^{-1} \text{ min}^{-1}$) were not significantly different (two-tailed two-sample t -test) from those obtained from pigeons without a mask ($12.4 \pm 2.3 \text{ ml STPD kg}^{-1} \text{ min}^{-1}$, Jensen and Bech, 1992). This indicates that the relative changes in the respiratory variables observed during the entry into hypothermia were not significantly influenced by the method used.

Air-sac gases

Two early studies of the composition of the air-sac gases in the pigeon reported widely differing values for the interclavicular air sac: 6.0 kPa and 4.1 kPa for P_{CO_2} and 11.8 kPa and 14.4 kPa for P_{O_2} (Soum, 1896; Plantefol and Scharnke, 1934, respectively). The divergence between the two studies was less for the abdominal air sac, for which the reported P_{CO_2} values were 2.5 kPa and 3.1 kPa and the P_{O_2} values 16.0 kPa and 15.2 kPa, respectively. In the earlier study no anesthesia was used. We can offer no explanation as to why these values should differ so markedly from the results reported here (Table 2).

In the goose (*Anser anser*, Scheid *et al.* 1989) the values of P_{CO_2} (5.2 kPa) and P_{O_2} (12.3 kPa) in the interclavicular air sac were very similar to the values reported here for the pigeon. The values for the abdominal air sac were very different, $P_{CO_2}=2.4 \text{ kPa}$ and $P_{O_2}=17.0 \text{ kPa}$, indicating that neopulmonic gas exchange in the goose is slower than that in the pigeon.

The higher RE values recorded for the abdominal air sac compared to those for the interclavicular air sac (Fig. 3) support the conclusion drawn from the data for the goose (Scheid *et al.* 1989) that the neopulmo plays a quantitatively more important role in the elimination of CO_2 than in the uptake of O_2 .

The cross-current arrangement of the blood capillaries lining the parabronchi of

birds makes it possible to have a higher partial pressure of CO_2 in the parabronchi than in the arterial blood. Such negative differences in the P_{CO_2} values between the arterial blood and the interclavicular air-sac gas have been reported for the duck (Powell *et al.* 1978), the domestic fowl (Piiper *et al.* 1970) and the goose (Scheid *et al.* 1989). The difference in the case of the goose was -0.9 kPa. In the present study of the pigeon, P_{ICCO_2} was 5.07 kPa at euthermy compared with an arterial partial pressure of CO_2 of 3.23 kPa (Jensen and Bech, 1992), a difference between the arterial blood and the interclavicular air-sac gas of -1.84 kPa. Although these values were obtained in different experimental series, they clearly indicate the effectiveness of the gas exchange mechanism of the avian lung.

Hypothermia

Few ventilatory data exist for birds in a state of torpor. Withers (1977a) studied two species of hummingbirds (*Selasphorus sasin* and *Calypte anna*) and the poorwill (*Phalaenoptilus nuttalli*). For all three species f and \dot{V}_I decreased dramatically during entry into torpor, whereas a slight decrease in V_T only was observed in the poorwill. V_T decreased by 22 % in the poorwill, far less than the eightfold decrease recorded in f . Our pigeons, in contrast, decreased V_T by 18 % and f by 20 % when entering shallow hypothermia (Table 1). During torpor, the poorwill reached a minimal T_b of 10°C associated with a tenfold reduction in \dot{V}_I . It would seem to be crucial for the poorwill to reduce f more than V_T in order to avoid increasing the relative dead space ventilation too much.

Bucher and Chappell (1989), using two different species of hummingbirds (*Selasphorus rufus* and *S. platycercus*), confirmed that the decrease in \dot{V}_I was only induced by reductions in f . Withers (1977a) found a decrease in $\dot{V}_I/\dot{V}_{\text{O}_2}$, whereas Bucher and Chappell (1989) found an almost twofold increase when the hummingbirds changed from euthermy ($T_b=40.6^\circ\text{C}$) to a state of torpor (minimal $T_b=12.2^\circ\text{C}$). The same authors also reported that torpor in hummingbirds is characterised by periods of apnea lasting up to 5 min. When entering torpor, the $\dot{V}_I/\dot{V}_{\text{O}_2}$ ratio of the poorwill was constant (Withers, 1977a).

In the pigeon, the decrease in $\dot{V}_I/\dot{V}_{\text{O}_2}$ (Fig. 1) on entry into hypothermia indicated an increase in P_{CO_2} in the lungs, leading to an elevated arterial partial pressure of CO_2 *in vivo*. This was confirmed by the results of the parallel study. Following a 4°C decrease in T_b , the total arterial CO_2 content increased by 16 %, which can be attributed to parabronchial hypoventilation and an increase in the solubility coefficient of CO_2 (β_{CO_2}) of 8 % (calculated from Reeves, 1976). Furthermore, this is in accordance with the observed increases in both P_{ABCO_2} and P_{ICCO_2} (Fig. 2).

The greater changes of partial pressures in the abdominal than in the interclavicular air sac may have been caused by several factors. During entry into hypothermia, a parabronchial hypoventilation was produced by decreases in both f and V_T , leading to an increased P_{CO_2} and a decreased P_{O_2} in the residual dead space air, thus inducing a change in the composition of the air that entered the parabronchi. This could have altered the composition of the gas in the abdominal

air sac more than in the interclavicular air sac, because the inspired air passes through the abdominal air sac before it enters the paleopulmo (Scheid *et al.* 1974) where the major part of gas exchange takes place.

Another factor that could have caused differential changes in the composition of the gas in the different air sacs is a relative redistribution of the air flow within the lung/air-sac system. Not all the air that enters the abdominal air sacs passes through the neopulmo; some of it may take a bypass route, thereby avoiding gas exchange in the neopulmo on inspiration (Scheid *et al.* 1989). A relative redistribution of the air passing into the neopulmo and that bypassing it to enter the abdominal air sacs directly could lead to a change in the composition of the air in this air sac without having much effect on the composition of the air in the interclavicular air sac. However, very little is known about the extent to which birds are able to regulate the air flow within their lung/air-sac system.

In mammals, most CO₂ retention leading to respiratory acidosis probably takes place at the beginning of entry into torpor, because a sudden decrease, of short duration, in the respiratory gas exchange ratio has been observed both in the deer mouse (*Peromyscus maniculatus*; Nestler, 1990) and in the desert ground squirrel (*Spermophilus tereticaudus*; Bickler, 1984). It is not clear whether this is also true for mammals entering shallow hypothermia. In the pigeon, in contrast, the respiratory acidosis apparently developed gradually with a constant pH *in vivo* when T_b decreased (Jensen and Bech, 1992). The present results confirm this view, i.e. the \dot{V}_I/\dot{V}_{O_2} ratio remained constant and the change in the composition of the air-sac gases resulted in constant gas exchange ratios during entry into hypothermia (Fig. 3). Thus, there was no indication that the changes in P_{CO_2} in the air sacs could have induced any sudden decline in arterial pH that could be responsible for an initial reduction in the metabolic rate. However, the gradual development of respiratory acidosis induced by the effective parabronchial hypoventilation may have had an effect on the metabolic rate at a later stage of entry into hypothermia.

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