Gas exchange in penguins during simulated dives to 30 and 68 m

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Gas exchange in penguins during simulated dives to 30 and 68 m. Am. J. Physiol. 225(6): 1467-1471. 1973.—Adelie and gentoo penguins were submerged and compressed in a chamber to depth equivalents up to 68 m. Lung and air sac volume upon compression averaged 165 ml/kg for Adelie and 160 ml/kg for gentoo penguins. Arterial N2 tensions increased to 3.5 ATA during 30-m dives and to 4.8 ATA during 68-m dives. PaO2 before the dive was 51 mm Hg, it rose abruptly to 50 mm Hg after submersion and compression, and after decompressing but before surfacing PaO2 fell to 35 mm Hg. Oxygen content of the thoracic air sac fell from 13.2 to 2% during a compression dive; PaO2 rose upon compression and then fell rapidly during the remainder of the dive. After ventilation on 100% O2, PaO2 exceeded 800 mm Hg during compression dives. These results show that gas exchange between the air sacs, lungs, and blood continues during deep dives. The main protection of these two species of penguin to the adverse effects of inert gas absorption appears to be an incapacity for prolonged dives and therefore prolonged exposure.

Adelie penguin; gentoo penguin; compression dives; arterial O2, CO2, and N2; air sac O2 and CO2 concentration

THE DEPTH AND DURATION of dives reported for some species of birds and the unusual structure of the bird respiratory system make them an interesting group to study and to compare with deep diving mammals in regard to effects of pressure on gas exchange in the lungs.

Most birds do not dive for more than 2-3 min (3), and the diving depth of only a few birds has been reported. Common loons, Gavia immer, and old squaws, Clangula hyemalis, have become entangled in nets at depths of 60 m (18). Emperor penguins, Aptenodytes forsteri, are exceptional. They dive for as long as 18 min and as deep as 265 m (8).

Unlike mammals most of the respiratory gas in birds is not contained in the gas exchanging area of the lung but is in the air sacs. The lung is a rather rigid structure attached to the dorsal portion of the ribs and vertebrae. The details of movement of air from the air sacs and through the lungs during normal ventilation have been described recently (1, 15). Experiments by Pickwell (14) have shown that in the duck gas exchange continues between the air sacs, lungs, and blood during dives of shallow immersions, and the O2 store of the air sacs is an important determinant in the duration of the dive. This is different from the seal which dives on partial expiration and in which the lung oxygen store is neither an important fraction of the total body O2 store nor an important determinant of the length of the dive (11, 16). In seals during deep dives gas exchange between the lungs and blood occurs for a proportionately short part of the time and blood N2 tensions remain low (19).

Field observations indicate that emperor, Adelie, Pygoscelis adeliae, and gentoo, P. papua, penguins dive on inspiration. If, like the duck, the air sac O2 store is an important factor regarding the length of dive, then during deep dives the inert gas tensions in the blood and tissues might be higher than those in the seal. No studies of the effect of pressure on gas exchange between the blood, lungs, and air sacs have been carried out on birds, and it cannot be assumed that gas exchange patterns would be similar to those that occur in shallow dives. The increased hydrostatic pressure occurring in deep dives may somehow interfere with gas exchange between the blood, lungs, and air sacs.

The intent of this study was to determine the changes in oxygen, carbon dioxide, and nitrogen tension of the blood during simulated deep dives in penguins, the most completely aquatic family of birds. To do this Adelie and gentoo penguins were compressed to 4 and 7.8 atm absolute (ATA), or an equivalent of 30-68 m sea water depth, in a completely water-filled chamber. Air sac and lung volume, arterial gas tensions, and air sac composition were determined during dives.

MATERIALS AND METHODS

Three Adelie penguins were collected near Palmer Station, Antarctica, and appeared to be nonbreeding birds. Their average weight was 4.3 kg. Three gentoo penguins were nonbreeding birds collected near Port Lockroy, Antarctica. Their average weight was 4.9 kg. No bird was kept for more than 6 days and both species fasted, except for water, while in captivity.

In order to dive the birds they were held in place on an aluminum plate by means of steel hoops which girdled the animal. The wings were left free. The plate was then fastened to steel angles attached to the wall of the compression chamber. The chamber was inclined at 20° so that it could be nearly filled with water and not immerse the head of the bird. The chamber was ventilated with an air pump until the dive, at which time it was completely filled using a
High-speed water pump. Pressure was applied with a hand hydraulic pump, and the amount of water required to achieve a given pressure was measured. In the absence of a penguin there was no measurable drop in pressure for 30 min at 4 ATA.

Since the bird is the only compressible object in the chamber, the volume of water needed to reach a given pressure is due to compression of the bird minus a small correction for chamber expansion. Thus, the chamber functions as a sensitive whole-body plethysmograph. Of 19 known gas volumes measured in this way, which ranged from 0.5 to 2.0 liters, the error averaged 0.5%.

The compressible portions of the penguin are the respiratory system, the air trapped in the feathers, and the gastrointestinal tract. Since the birds voluntarily compress their feathers to a layer only 5 mm thick upon diving, which results in a very tight layer, the amount of air trapped is small and no correction was made. Based on differences in volume of water displaced in three birds before and after washing the feathers with a detergent, this introduces an error in our measurements of about +10%. It was not possible to determine the amount of gas in the gastrointestinal tract. Presumably it is small compared to the respiratory system.

Prior to any blood sampling the birds were practice dived a number of times. During the dives the behavior of the penguins was observed through one of the four viewing ports. The birds were subjected to only four or five dives to mine the amount of gas in the gastrointestinal tract. Presumably it is small compared to the respiratory system.

Blood samples were obtained from a polyvinyl chloride catheter of 3.6 mm od placed in the descending aorta via the femoral artery. The catheter was inserted after administering Xylocaine, a local anesthetic. Exact location of the catheter tip was determined by radiography, and it was 2 or 3 cm distal to the aortic arch.

The catheter passed through the compression chamber wall by means of a Swagelok fitting. On the outside it was connected to a pressure syringe for flushing with normal saline. Upon removal of the flushing syringe, blood samples were drawn in 1-ml tuberculin syringes, the dead space of which was filled with heparin and glycerin. The blood-filled syringes were sealed and stored at 1 ATA in an ice water bath. Those analyzed for oxygen tension were done on the average within 11 min.

Blood nitrogen was analyzed with a 5-ml syringe extractor according to the method of Scholander et al. (17) except the blood was degassed by vacuum extraction. The entire blood sample and all gas bubbles that had developed during storage were transferred to the analyzer, and the O₂ and CO₂ were absorbed with a basic hydrosulfite solution. The N₂ volume was quantitatively measured in the calibrated capillary tip of the extractor. The mean N₂ solubility of the blood of four penguins determined in this way was 0.128 ml N₂ x ml⁻¹ blood x atm⁻¹ N₂, n = 18, coefficient of variation (CV) = 13.4%. Distilled water equilibrated at 1, 4, and 5.8 ATA and sampled similarly to blood drawn from the penguins and analyzed by this method averaged 6.3% (n = 10, 5, and 6, respectively) less than previously reported values for N₂ solubility (4). The CV was 2.3, 5.8, and 0.7% for 1, 4, and 5.8 ATA.

Blood oxygen and carbon dioxide tensions were analyzed with a Radiometer blood microsystem model BMS3B and digital pH meter model PHM72. Due to the high gas tensions in the arterial blood of birds during compression, there was some degassing of the samples stored in the syringes. Because of this tension measurements of O₂ and CO₂ are qualitative estimates rather than quantitative measures. Dog blood equilibrated with compressed air at 4 and 6 ATA and analyzed at ambient pressure resulted in oxygen tensions 46 and 55% below theoretical values. Because of the buffering capacity of blood, the error for CO₂ is probably not great.

When the birds were compressed after ventilation on 100% oxygen, the blood oxygen tension exceeded the manufacturer's limit of 800 mm Hg for the analyzer, and again the analysis is considered only a qualitative estimate of actual oxygen tension. Tensions observed above 800 mm Hg are reported as off scale. Even though the measurements are subject to error because of degassing of the samples, the results are conclusive as will be seen later.

Air sac gas was sampled in a similar fashion to blood. Analysis of the gas sample was with a Scholander water-gas analyzer (17).

During the dive the electrocardiogram was used as an instantaneous assessment of the condition of the bird. Needle electrodes were placed subcutaneously near the axillae, and the heart rate was monitored on a Cambridge direct printout recorder.

RESULTS

The blood N₂ tensions, calculated from content determinations, show that during 4-ATA dives N₂ tension rose 2-4 times its original level; the average value was 2.7 ATA (Fig. 1). The higher values were close to an estimated equilibrium tension between the blood and lungs, assuming a nitrogen fraction of 0.9 in the lungs, and the blood passing through the lungs is completely equilibrated. During 7.8-ATA dives tension increased 2.5-5 times. The average tension was 3.5 ATA.

![FIG. 1. Pattern of arterial N₂ tension changes during 8 4-ATA (upper) and 6 7.0-ATA (lower) dives (30 and 68 m water depth) in Adelie and gentoo penguins. Dotted line bridging CP and DCP columns equals estimated equilibrium tension of blood if it matched air sac N₂ partial pressure, assuming N₂ fraction of air sacs is 0.9. During 7.8-ATA dives pressure fell during compression to 6.8 ATA. Beginning and end of dive (arrows) and compression (CP) and decompression (DCP) represent average schedule for all dives.](http://ajplegacy.physiology.org/DownloadedFrom)
During surface dives the CO₂ tension rose gradually from an average predive level of 32 mm Hg to a maximum of 59 mm Hg (Fig. 2). The average P_{aco₂} shortly before compression dives was 31 mm Hg. The P_{aco₂} appeared to rise abruptly during compression and remained elevated until decompression at which time it decreased even though the animal was still submerged. The average P_{aco₂} during compression was 30 mm Hg and shortly after decompression, but before surfacing, P_{aco₂} averaged 35 mm Hg. The P_{aco₂} 1.5 min after surfacing averaged 32 mm Hg. The degassing results in estimates which are lower than real tensions, but the large CO₂ reservoir of the blood due to its buffering capacity probably keeps this error small.

Arterial oxygen tension (P_{ao₂}) before diving averaged 79 mm Hg. Thirty to 40 sec before diving, as the water level began to rise in the chamber, the birds would hyperventilate, which probably raised the oxygen tension slightly just before submergence. Shortly after compression the P_{ao₂} was considerably above predive values, despite the fact that the bird had been breath holding for about 1.5 min (Fig. 3). The exact P_{ao₂} is unknown because the supersaturated blood would partially degas when reduced to 1 ATA after it was drawn into the syringe. Of the sigmoid nature of the hemoglobin dissociation curve, the low P_{ao₂} values determined later in the compression are nearer real values than the high values at the beginning. P_{ao₂} was slightly lower after decompression and within 1.5 min after surfacing P_{ao₂} averaged 85 mm Hg, slightly higher than the predive level.

Before some dives the penguins were ventilated 20–30 min on 100% oxygen. The average P_{ao₂} just before diving was 370 mm Hg, if one exceptionally low value is ignored. After increasing pressure, oxygen tensions were off scale and remained off scale during the period of compression (Fig. 3).

The air sac and lung volume of penguins at the beginning of a dive averaged 165 ml/kg body wt (STPD) for the Adelie and 160 ml/kg for the gentoo (Table 1). This is somewhat higher than the 137 ml/kg determined by Scholander (16) for a gentoo penguin that weighed 6 kg and probably had some subcutaneous blubber.

The gas composition of the left intrathoracic air sac in one Adelie penguin fell from an average O₂ concentration of 13.2% before the dive to 4.5% after 2.5 min of submersion. During compression dives of 4 ATA, the concentration fell to 2% after 2.5 min of submersion, the last 2 min of which were at pressure. The fall in O₂ concentration appeared more rapid during the 4-ATA dives (Fig. 4). Simultaneous CO₂ and N₂ concentration changes were from predive levels of 4.2% and 82.4%, respectively, to 6.0 and 89.5%, respectively, after 2.5 min of submersion. During 4-ATA submersions CO₂ and N₂ concentrations changed from similar predive levels as before to 2.5 and 95.5%, respectively, after 3.5 min of submersion (Fig. 4).

**DISCUSSION**

During 4-ATA dives the measured N₂ tension increased up to 4 times, and after compressions to 7.8 ATA it was up to 5 times more than original tensions (Fig. 1). Such high N₂ tensions as observed while the animals were compressed must be due to a substantial amount of exchange between the blood and lungs. The greater disparity between the
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in men exposed to repeated breath-hold dives to relatively shallow depths of 20-40 m and short durations of about 2 min (2, 13). Further studies of penguins subjected to similar dive schedules would be of interest.

The pattern of CO2 exchange between the lungs and blood during deep dives is similar to the observations of Lanphier and Rahn (10) who were studying human divers. If the dive is deep the partial pressure of CO2 in the lung rises to a tension above that of returning mixed venous blood. When this occurs CO2 exchange reverses and CO2 diffuses from the lungs to the blood. This condition is indicated in penguins by the abrupt rise in Pao2, shortly after compression (Fig. 2). Upon decompression, the expansion of lungs and air sacs results in a drop in partial pressure of CO2 and the blood-lung CO2 gradient is again reversed and CO2 diffuses in the normal direction. This results in a fall in Pao2 even though the bird is still submerged. These changes are more marked than the data show because the measured CO2 tensions are lower than actual values for reasons discussed earlier.

The change in air sac composition also reflects this gradient reversal. During 1-ATA dives the CO2 concentration rises from 4.2% up to 6% after 2.5 min of submersion as CO2 diffuses into the air sacs. During 4-ATA dives, the CO2 concentration falls after compression and is only 2.5% after 3.5 min of submersion (Fig. 4). The faster diffusing O2 and CO2 enter the blood more rapidly than N2, resulting in a decline in their proportions within the air sacs.

The rise and fall in Pao2 (Fig. 3) and the fall in air sac O2 concentration (Fig. 4) during the compression period of the dives also show that the lungs and air sacs are exchanging with the blood during the entire period. The Pao2 of birds compressed to 4 and 7.8 ATA after first ventilating on 100% O2 was off scale, over 800 mm Hg, during the entire compression period. Using the ordinary pulmonary shunt equation (12), we can predict what percent shunting would be necessary for Pao2 to fall below 800 mm Hg if we assume that: 1) the blood O2 capacity is 200 ml/liter, 2) O2 pressure in the parabronchi is nearly 3,000 mm Hg during a 4-ATA dive, and 3) the O2 content of mixed venous blood is 5 vol% less than arterial blood or 175 ml/liter. (The a-v difference is not known in penguins during a dive, but it has been observed to remain constant around 5 vol% in diving seals (6)). We calculate that shunting would need to be between 50 and 60%.

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