

## HEART RATE AND AEROBIC METABOLISM IN HUMBOLDT PENGUINS, *SPHENISCUS HUMBOLDTI*, DURING VOLUNTARY DIVES

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*Accepted 17 August 1983*

### SUMMARY

Heart rate and aerobic metabolism have been recorded from three Humboldt penguins, *Spheniscus humboldti*, freely diving on a freshwater pond ( $9 \times 4.6 \times 2.7$  m deep), using an implanted radiotransmitter and an open circuit respirometer. Oxygen uptake at mean dive duration (46.2 s) was 26% greater than the resting value, but the difference was not statistically significant. Heart rate was also similar to the resting value. It is concluded that voluntary dives of penguins are completely aerobic and that oxygen stores are sufficient to allow metabolism to continue at the rate estimated in the present study for 2.27 min during voluntary submersion. This is longer than that calculated for tufted ducks, probably because the penguins are more efficient at underwater locomotion and because they are almost neutrally buoyant.

### INTRODUCTION

It has recently been demonstrated that aerobic metabolism of tufted ducks, during voluntary submersion, is similar to that during maximum sustained swimming activity in a water channel. At the same oxygen uptake, however, heart rate is significantly lower during diving than during swimming but substantially higher than during forced submersion of the head (Woakes & Butler, 1983). It has been suggested that the cardiovascular and metabolic responses to voluntary diving in ducks are a balance between the 'classical' response to forced submersion (bradycardia, vasoconstriction except in CNS and heart, anaerobiosis) and the response to exercise (tachycardia, vasodilation in active muscles) with the bias towards the exercise response (Butler, 1982).

Ducks have to work continuously to remain submerged. In fact, cessation of leg beating leads to rapid, passive surfacing as a result of the animals' positive buoyancy (Butler & Woakes, 1982a). Penguins on the other hand, are much better adapted to an aquatic existence and the 'exercise' component of their physiological responses to underwater activity may not be as great as in ducks.

It was decided, therefore, to record heart rate, using radiotelemetry, during various

types of activity (particularly voluntary diving) in Humboldt penguins. It was not possible to record data from these birds swimming in a water channel (they were too large), but it was possible to measure oxygen uptake in resting birds and to estimate it at mean duration of voluntary dives.

#### MATERIALS AND METHODS

Three Humboldt penguins, *Spheniscus humboldti*, that ranged in mass from 4.3–5.9 kg were used. They were obtained from a commercial dealer and kept on an outside, freshwater pool (9 × 4.6 × 2.7 m deep). They were fed frozen sprats which were thrown onto the pool and for which the penguins had to dive. Each penguin was also fed one Mazuri fish eater tablet [B.P. Nutrition (U.K.) Ltd, Witham, Essex] per day. The pool was emptied and refilled regularly in order to prevent the water becoming too opaque.

Initially, recordings of heart rate were made from each bird during various types of activity, but particularly during natural dives, by way of a small, purpose-built, single channel, PIM radio transmitter (Butler & Woakes, 1982a). The bird was anaesthetized with 3 or 4% Halothane (I.C.I. Ltd, Macclesfield, Cheshire) in a mixture of 10% O<sub>2</sub> in air. The sterilized transmitter (see Butler & Woakes, 1979) was placed in the abdominal cavity and separate electrodes were positioned either side of the heart. After the implantation, an injection of ampicillin (30 mg kg<sup>-1</sup> i.m. Penbritin, Beecham, Brentford, Middx) was administered and the bird was released onto the pool when it had fully recovered (usually 3–4 h later). Recordings from the free range birds were made as described by Butler & Woakes (1979). As well as recording heart rate during voluntary behaviour, it was also monitored during artificially extended voluntary dives during which the penguin was discouraged from surfacing by holding a net over the pool as it approached the surface. Data were stored on tapes, decoded through a purpose-built demodulator (Woakes, 1980) and hard copies made on a two-channel pen recorder (Ormed Ltd, Welwyn Garden City, Herts). Heart rate was determined by an Ormed instantaneous rate meter.

Gas exchange was measured by a way of a large (100 l) open circuit respirometer similar to that described by Woakes & Butler (1983). The whole of the surface of the pool was covered with netting at a depth of 7 cm except for an area in one corner which was covered by the respirometer. This was divided by a perforated sheet of acrylic into two chambers. The larger section (80 × 65 cm) held a single penguin and was large enough to allow the bird sufficient room to move about freely, i.e. to preen and to dive. The smaller chamber housed six fans that ensured complete and rapid mixing of the air in the respirometer ( $\tau < 1.5$  s). Air was drawn through the respirometer at 40 l min<sup>-1</sup> and the fractional concentrations of oxygen and carbon dioxide in the outlet gases were sampled by a mass spectrometer (MGA 007, Centronics Ltd, Croydon, Surrey). A rotary valve switched the mass spectrometer gas input from air leaving the respirometer to inlet air for 2 s every 30 s. This enabled any drift in the mass spectrometer to be corrected during subsequent analysis of the data. By injecting known volumes of the gases it was found that, although there was no detectable loss of oxygen from the system, sufficient carbon dioxide was absorbed by the water when the bird was in a semi-resting state (i.e. not completely inactive) to make calculations

of CO<sub>2</sub> production inaccurate. They were not, therefore, performed except for those instances when gas exchange increased abruptly just before diving and the first exhalation upon surfacing. In these instances there was a rapid, transient change in gas exchange. During the latter, the penguin exhaled rapidly above water and there was, therefore, little chance of any CO<sub>2</sub> from this first exhalation being absorbed. Output from the mass spectrometer was recorded on a two-channel Ormed pen recorder for subsequent analysis. All equipment for gathering the data, and calibrating the mass spectrometer etc., were accommodated in a wooden hut close to the corner of the pond where the respirometer was located. The penguin was fed by placing fish on the bottom of the pond in the diagonally opposite corner.

Dives often occurred in a series and, using the mathematical technique described by Woakes & Butler (1983), it was possible to calculate the amount of oxygen consumed in the interval between dives as well as during other forms of activity (rest, preening etc.). Assuming that the bird fully replenished its oxygen stores before any dive, the oxygen uptake between dives should depend on the duration of the dive (through the repayment of the physical oxygen debt) and the duration of the interval. Multiple linear regressions of the volume of oxygen consumed during the interval against dive duration and interdive duration allow the consumption of the gas during the dive and interval to be estimated (see Woakes & Butler, 1983). These assumptions were validated by the significant correlations found in the regression analyses. Oxygen uptake during rest was measured by using the respirometer in the standard open circuit condition.

The pen recordings of the output from the mass spectrometer were digitized by a GTCO Digipad 5 (S.S.I. Ltd, Marlborough, Wilts) and the gas volumes calculated and analysed on a B.B.C. Model B microcomputer. Measurements were also made of the volumes of oxygen depleted and carbon dioxide added to the first exhalation after surfacing, as this was very evident on the recordings (Fig. 1). All gas volumes are corrected to STPD.

Mean values of a variable were obtained for each penguin ( $N$  for each bird are given in the Results section). These mean values were then averaged and the standard error (S.E.) of this final mean was obtained. Significance of differences was calculated by Student's  $t$ -test or, when appropriate, the method of paired comparisons. Results were considered significant at the 95 % confidence level ( $P < 0.05$ ).

## RESULTS

There were large variations in heart rate of free range penguins. The lowest mean value of  $121 \pm 5$  beats  $\text{min}^{-1}$  ( $N = 4$  in all birds) was recorded when the birds stood motionless on land. When they were floating inactively on water, mean rate was higher at  $139 \pm 5$  beats  $\text{min}^{-1}$  ( $N = 2, 3$  and  $4$ ). The highest values were recorded when the birds ran and gave a mean rate of  $245 \pm 24$  beats  $\text{min}^{-1}$  ( $N = 2, 2$  and  $4$ ). Dives often occurred in a series. Before the first dive of such a series, the penguins sometimes swam gently on the surface with their eyes submerged (Fig. 2). Diving was always achieved by the bird gliding effortlessly under the water from such a position. Whether diving occurred immediately upon submersion of the head or not, heart rate merely became steady as soon as the head was submerged, i.e. sinus arrhythmia

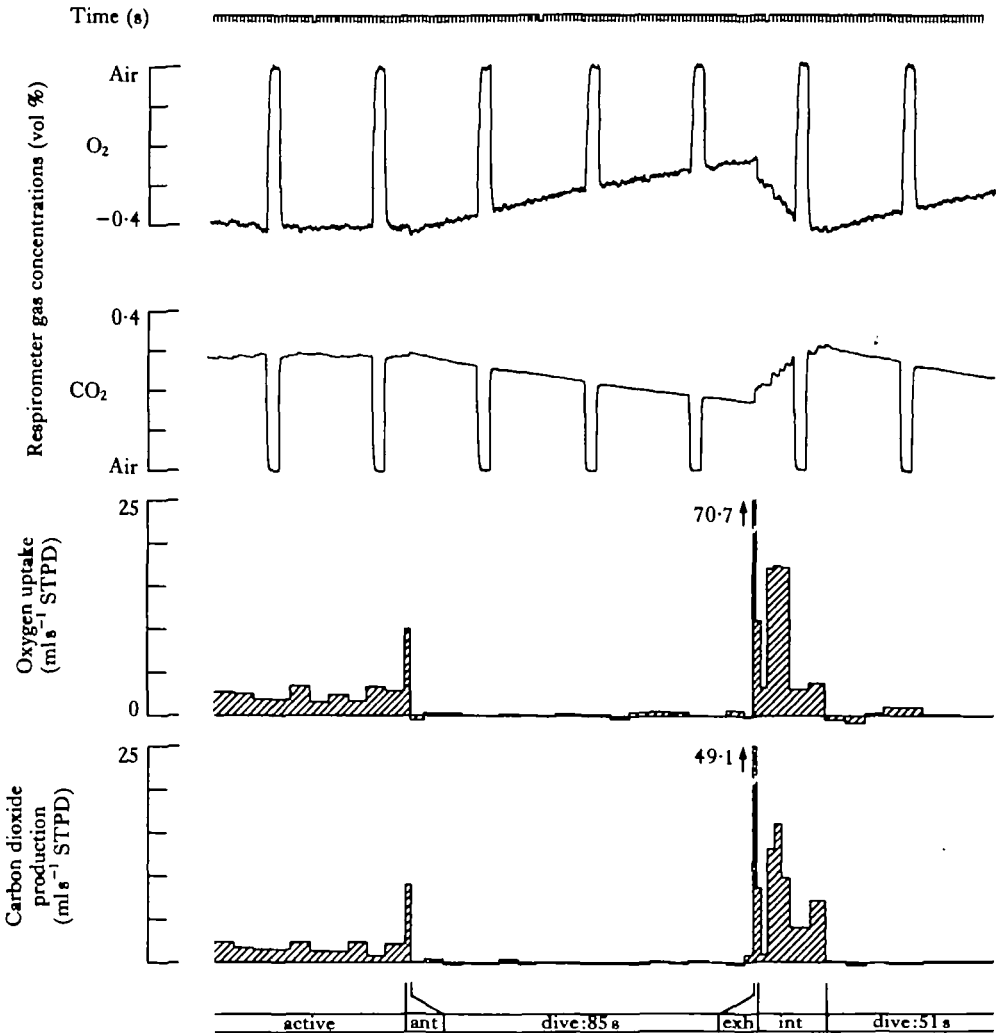


Fig. 1. Oxygen uptake and carbon dioxide production of a Humboldt penguin (4.5 kg) before and after one of the longest voluntary dives beneath the covered pond. Instantaneous values of gas exchange were computed from the changes in gas concentrations in the respirometer as described in the text. Note the brief increase in gas exchange immediately preceding the dive (ant) and also the large changes in gas concentrations associated with the first exhalation (exh) upon surfacing (actual values are given next to histogram). Oxygen consumption at mean dive duration is estimated from the total oxygen uptake during the intervals (int) between dives (see Materials and Methods).

disappeared (Fig. 3). During all voluntary dives, from which the bird was not discouraged from surfacing, there was no significant reduction in heart rate below the resting levels (Table 1). Mean dive duration of the five longest such dives from each penguin was 36.4 s. Even during the longest (50 s) heart rate varied little (Fig. 3). Attempts were made to extend voluntary dives by waving hand nets over the surface of the water. It was thus possible to obtain from two penguins four dives in excess of 60 s duration (mean 63.7 s). Up to 50 s submersion heart rate was, as predicted from the fully spontaneous dives, similar to that at 30 s (119 beats min<sup>-1</sup> and 125 beats

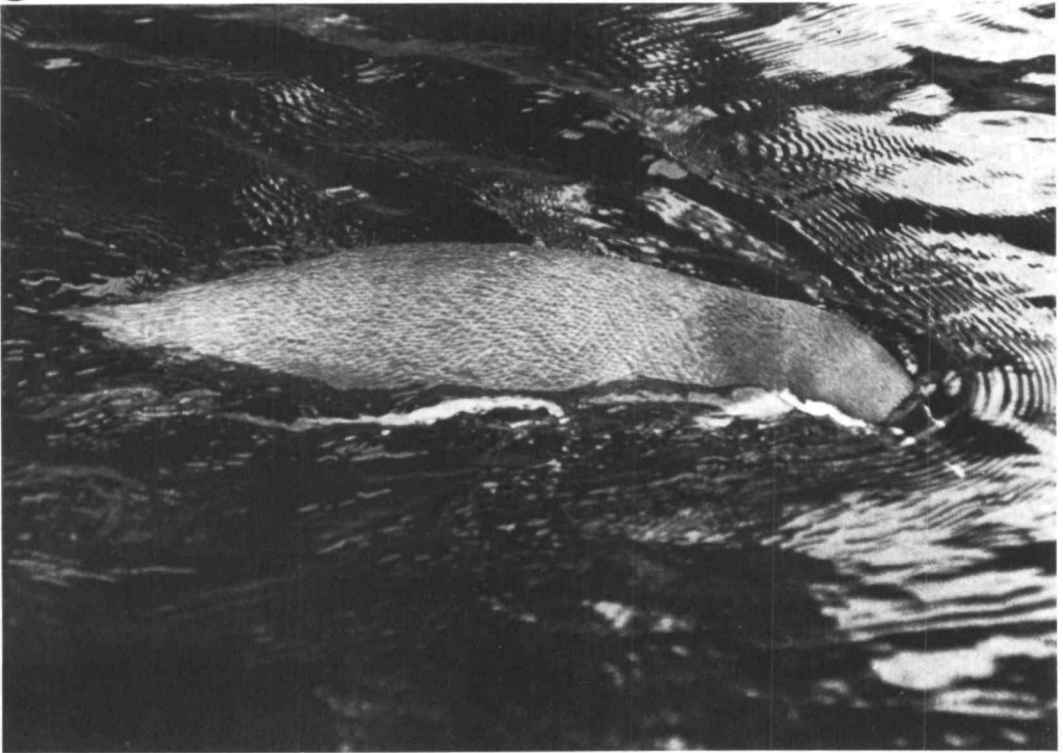


Fig. 2. Humboldt penguin swimming on the surface of the pond with its eyes under water before submerging completely.



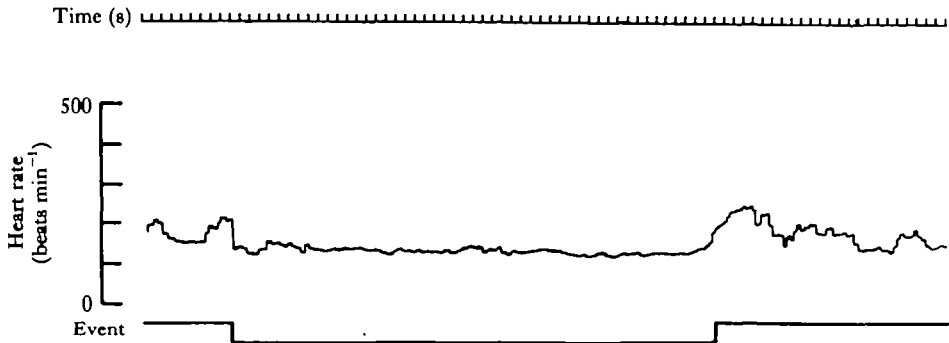


Fig. 3. Heart rate of Humboldt penguin (4.5 kg) before, during and after the longest recorded, fully spontaneous dive (50 s). Duration of dive indicated by downward deflection of the event marker.

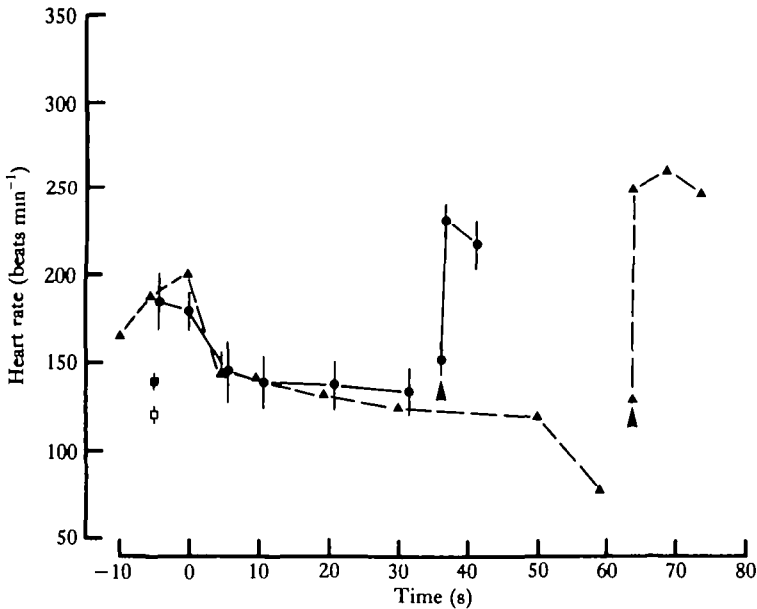


Fig. 4. Mean values of heart rate from three Humboldt penguins at rest and during voluntary dives. Mean values were initially obtained for each penguin from  $N$  observations on each animal. These means were then averaged and, where appropriate, the s.e. obtained. Five longest fully spontaneous dives from each bird ( $\bullet$ ), voluntary dives from which two birds were discouraged from surfacing by a hand-held net ( $\blacktriangle$ ,  $N = 2$ , 2). s.e. was not calculated when only two birds were used ( $\blacktriangle$ ). For the other mean values, vertical lines indicate s.e. of mean (where absent, s.e. is within the thickness of the symbol). Submersion occurred at time 0 and surfacings occurred at the times indicated by the arrowheads ( $\blacktriangle$ ). During both types of dives heart rate increased before the birds broke surface. Also included are mean values ( $\pm$  s.e.) of heart rate when the three birds were resting on water ( $\blacksquare$ ,  $N = 2$ , 3, 4) and when resting on land ( $\square$ ,  $N = 4$ , 4, 4).

$\text{min}^{-1}$  respectively). At 60 s, however, it had fallen dramatically to 78  $\text{beats min}^{-1}$  (Fig. 4). When waving the hand nets, the investigators stood near the edge of the pool and with clear water it was possible to get good views of the birds under water. A notable feature was that the penguins were able to remain almost motionless at the bottom with little or no movements of the flippers.

Table 1. Mean ( $\pm$  S.E.) of measured variables in three Humboldt penguins at rest and during various types of activity on an outside pond (2.7 m deep)

	Resting	Preening	Dives	Between dives	Anticipation before a dive	First exhalation upon surfacing
Oxygen consumption (ml s <sup>-1</sup> STPD)	0.993 $\pm$ 0.023 (N = 5, 5, 8)	2.104 $\pm$ 0.150 (N = 1, 3, 8)	1.25 $\pm$ 0.12 (r = 0.57 $\pm$ 0.028)	1.69 $\pm$ 0.09 (r = 0.64 $\pm$ 0.014)	19.2 $\pm$ 1.63 (ml)	41.9 $\pm$ 2.58 (ml)
Carbon dioxide (ml s <sup>-1</sup> STPD)	—	—	—	—	18.9 $\pm$ 2.48 (ml)	26.4 $\pm$ 1.6 (ml)
Respiratory quotient	—	—	—	—	0.97 $\pm$ 0.05	0.63 $\pm$ 0.01
Duration (s)	—	—	46.2 $\pm$ 3.2 (N = 56, 67, 73)	20.1 $\pm$ 2.6	0.94 $\pm$ 0.05 (N = 3, 5, 11)	1.84 $\pm$ 0.05 (N = 37, 49, 50)
Water temperature (°C)	18.0 $\pm$ 0.2					
Heart rate (beats min <sup>-1</sup> )	(W) 139 $\pm$ 5 (N = 2, 3, 4) (L) 121 $\pm$ 5 (N = 4, 4, 4)	178 $\pm$ 20 (N = 4, 4, 3)	134 $\pm$ 15 (N = 5, 5, 5)	—	—	231 $\pm$ 10 (N = 5, 5, 5)
Duration(s)			36.4 $\pm$ 4.5 (N = 5, 5, 5)			
Mass (kg)	4.6 $\pm$ 0.11					

Mean values of a variable were obtained from *N* observations on each penguin. These means were then averaged and the S.E. obtained.

The partial correlation coefficients (*r*) from the multiple regressions (see Materials and Methods) are given beneath the values for oxygen consumption at mean dive duration and at mean inter-dive duration.

Heart rate was recorded during a different set of observations, and the mean dive duration and heart rate during dives refer to the five longest fully spontaneous dives for each bird. Resting heart rates are for when the birds were on water (W) and on land (L). The value during diving refers to 5 s before surfacing, i.e. before the anticipatory increase in heart rate occurs.



Surfacing from all fully spontaneous dives was preceded by an increase in heart rate, and a further increase occurred as the birds broke the water surface (Fig. 4). This post-dive tachycardia was greater after the artificially extended dives. The post dive tachycardia often resulted in elevation of heart rate above resting level before second and subsequent dives of a series.

Measured oxygen consumption for all three penguins when inactive in the respirometer was almost  $1 \text{ ml s}^{-1}$ . Resting values were obtained when the bird was seen to be inactive and had consumed oxygen at a steady rate for at least 8 min. Measurements were made for 1 min at the end of this period. Such criteria were rarely met and the numbers of observations ( $N$ ) from each bird were 5, 5 and 8. On a few occasions all three birds showed a clear increase in gas exchange just before submersion (Fig. 1, Table 1). During these periods ( $0.94 \pm 0.02 \text{ s}$ ,  $N = 3, 5$  and  $11$ ) oxygen uptake was  $19.2 \pm 1.6 \text{ ml}$  and carbon dioxide production was  $18.9 \pm 2.5 \text{ ml}$  giving a transitory respiratory quotient (RQ) of  $0.97 \pm 0.05$ . During the interval between dives beneath the covered pond, oxygen uptake was  $6.15 \pm 0.35 \text{ ml s}^{-1}$  over a mean period of  $20.1 \pm 2.6 \text{ s}$  ( $N = 56, 67, 73$ ). Of this total, the rates of oxygen metabolism at mean dive duration and at mean interdive period, derived from the regression analysis, are given in Table 1. That for mean dive duration is not significantly different from resting, whereas that for mean interdive interval is a significant 70% greater than resting. During the first exhalation upon surfacing, oxygen was depleted at a rate of  $22.8 \text{ ml s}^{-1}$  ( $N = 37, 49, 50$ ) and carbon dioxide was added at a rate of  $14.3 \text{ ml s}^{-1}$ , giving a respiratory quotient of 0.63 (Table 1). This first exhalation was clearly visible on the traces of gas concentrations inside the respirometer box (Fig. 1).

#### DISCUSSION

Penguins, like other aquatic birds, respond to forcible submersion of the head by developing a progressive, rather severe bradycardia (Scholander, 1940; Millard, Johansen & Milsom, 1973; Kooyman, 1975). Millard *et al.* (1973) noted that the cardiovascular adjustments they recorded during voluntary diving in penguins could not be 'readily compared' with those obtained from restrained birds that were forcefully submerged. In fact they first suggested that when the penguins were diving normally the results obtained were a 'composite of diving and exercise responses'. Their data also indicated that metabolism may be different during voluntary compared with forced dives. During the former there was 'no discernable drop' in  $\text{PaO}_2$  whereas during the latter, the change in  $\text{PaO}_2$  was 'more marked'. Despite these findings Kooyman (1975), when calculating dive duration of penguins from their usable oxygen stores, stated that during diving, aerobic metabolism is much less than in the resting animal. The present results indicate quite clearly that this is not the case, but even so, they appear to be quantitatively at variance with recently-acquired data from freely diving birds.

Kooyman, Davis, Croxall & Costa (1982) found that for king penguins, *Aptenodytes patagonica*, metabolic rate (determined from the turnover of tritiated water) during foraging at sea off S. Georgia Island was 2.8 times standard metabolic rate (SMR). Temperature of the water was approximately  $2^\circ\text{C}$  (J. P. Croxall, personal communication) and from the work of Kooyman, Gentry, Bergman & Hammel

(1976) on Adélie penguins, oxygen uptake of inactive birds at this water temperature could be 3.8 times that recorded when they are resting in air at 13–15°C. In other words, comparing metabolic rate of animals foraging in water at 2°C with SMR (which is recorded from starving animals at their thermoneutral environmental temperature) is not comparable to recording oxygen uptake from animals that are resting and diving in water at the same temperature. Having said that, the present measurement of oxygen uptake for inactive Humboldt penguins in water at 18°C is lower than would be predicted from the work of Kooyman *et al.* (1976) on Adélie penguins (0.99 ml s<sup>-1</sup> compared with 1.52 ml s<sup>-1</sup> respectively for 4.6-kg animals). Maybe, therefore, more work needs to be done on the effect of water temperature on metabolic rate in penguins (preferably unrestrained). Nonetheless, using the data from Adélie penguins, Butler & Jones (1982) calculated that, for king penguins, metabolic rate during foraging at 2°C is 74% of that during periods of inactivity when in water at a similar temperature.

As mentioned in the Introduction, aerobic metabolism of tufted ducks increases considerably above the resting value during voluntary diving (Woakes & Butler, 1983). This must largely result from the work needed to overcome the positive buoyancy of these birds. Much effort is involved in submersion itself and continual leg movements are required to maintain the duck under water (Butler & Woakes, 1982a). The drag coefficient of penguins is certainly low (Clark & Bemis, 1979; Nachtigall & Bilo, 1980), but the fact that they need exert little apparent effort to submerge or to remain submerged, must be major factors in their aerobic metabolism during diving being similar to the resting value. Interestingly, only a small increase in aerobic metabolism above the resting value was noted in a male harbor seal during voluntary dives in the laboratory (Craig & Päsche, 1980).

Penguins and seals are therefore quite efficient when swimming under water, although when walking fast the energy cost of locomotion in Adélie penguins is relatively high and oxygen uptake can be over 6.4 times resting (Pinshow, Fedak & Schmidt-Nielsen, 1977). Indeed, some of the highest heart rates were recorded when birds in the present study were walking fast (running). The fact that during voluntary diving, both heart rate and oxygen uptake are similar to the resting values, but that heart rate is substantially above that recorded during forced diving (Millard *et al.* 1973; Kooyman 1975), indicates that, as with tufted ducks, the metabolic and cardiovascular adjustments to voluntary dives are different from those for forced dives (Woakes & Butler, 1983). For the ducks, there is good evidence to suggest that voluntary dives are completely aerobic. Certainly, there is sufficient usable oxygen stored in the body to enable metabolism to continue for almost twice the duration of most voluntary dives (Keijer & Butler, 1982; Butler & Woakes, 1982b). Using the values calculated by Kooyman (1975), usable oxygen stores of a 4.6-kg penguin are 170 cm<sup>3</sup> which, if used at the rate estimated in the present study, would enable the animal to remain submerged, and completely aerobic, for an average of 2.27 min. It is therefore proposed that, on average, voluntary dives of less than 2.3 min duration are aerobic in nature. Data from chinstrap penguins freely diving off Signy Island, South Orkneys, indicate that at night the birds dive to less than 45 m and for an average of approximately 1.6 min (Lishman & Croxall, 1983). Active swimming to such depths may cause aerobic metabolic rate to be higher than that estimated in the present study.

Unlike the situation in ducks, there was not the dramatic increase in heart rate (and presumably, respiratory frequency) before the first dive of a series in penguins, but there was a clear increase in gas exchange (and, therefore, loading of the oxygen stores) before some dives. This was for a much shorter duration than in tufted ducks (cf. Woakes & Butler, 1983) which, together with the high RQ, indicated that there was one deep inspiration followed by an expiration. If, like emperor penguins (Kooyman, Drabek, Elsner & Campbell, 1971), Humboldts dive on inspiration, there would also be a subsequent filling of the respiratory system before submersion. Also, like emperor penguins, the Humboldts did not appear to exhale under water, so the expiration upon surfacing was the first expulsion of air from the respiratory system since submersion. The large depletion of oxygen in the respirometer associated with the first exhalation demonstrated that oxygen in the respiratory system had been used during the preceding dive, and the low RQ indicated that carbon dioxide had been stored in the blood and tissues as suggested by Scholander (1940).

Clearly, there is a need for much more work to be done on these most aquatic of birds, but it does appear as if they are similar to ducks in their physiological responses to diving, with voluntary dives normally being completely aerobic. The large drop in heart rate at the end of voluntary dives, from which the penguins were discouraged from surfacing, indicates that like tufted ducks (Butler, 1982), penguins can switch to the oxygen conserving 'classical' response during natural diving behaviour. However, they are able to remain submerged and aerobic longer than ducks because they are more efficient at underwater locomotion. This improved efficiency is probably related mainly to their being almost neutrally buoyant.

The authors wish to thank Diane Williams for her assistance. This work was supported by SERC.

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