SWIMMING AND DIVING IN TUFTED DUCKS, *AYTHYA FULIGULA*, WITH PARTICULAR REFERENCE TO HEART RATE AND GAS EXCHANGE

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SUMMARY

In six tufted ducks there was a linear relationship between heart rate and oxygen consumption when swimming at different velocities. Mean oxygen consumption at mean duration of voluntary dives was 3·5 times resting and not significantly different from that at maximum sustainable swimming speed. Contrary to an earlier report (Prange & Schmidt-Nielsen, 1970), leg beat frequency increased with increased swimming speed.

Although heart rate at mean dive duration was 51% higher than the resting value, it was a significant 59 beats min^{-1} lower than predicted from the heart rate/oxygen consumption relationship obtained during swimming. This relationship is, therefore, of no use for predicting oxygen consumption from heart rate during diving, nor incidentally during transient changes during air breathing.

It is concluded that during voluntary diving in tufted ducks there is a balance between the cardiovascular responses to forced submersion (bradycardia, selective vasoconstriction) and to exercise in air (tachycardia and vasodilatation in active muscles), with the bias towards the latter.

INTRODUCTION

When the head of a duck is placed under water there is a substantial reduction in heart rate, redistribution of blood towards the oxygen dependent tissues (heart and CNS) and a reduction in aerobic metabolism. The reduction in heart rate is largely mediated by the carotid body chemoreceptors (see Butler & Jones, 1982; Butler, 1982 for reviews). During natural dives of pochards or tufted ducks, there is not a maintained reduction in heart rate (Butler & Woakes, 1976, 1979). Before the first dive of a series, heart rate and respiratory frequency increase. Upon submersion there is an instantaneous reduction in heart rate below the pre-dive level, but then it increases, over a period of approximately 6 s, and remains close to this value for the rest of the dive, which may be in excess of 30 s (Butler & Woakes, 1979; Butler, 1980). Heart rate, during the later stages of natural submersion, is similar to that recorded during high levels of swimming activity on an outside pond (Butler & Woakes, 1982a). During exercise in air, heart rate is a good indicator of oxygen consumption (Bamford

& Maloiy, 1980), so it is likely that, during natural submersion, oxygen uptake is not reduced, but is elevated above the resting value. The fact that heart rate is significant ly higher at the end of relatively long (>20 s) natural dives, following bilateral denervation of the carotid bodies (Butler & Woakes, 1982b), indicates that there is, actually, a slight inhibitory effect on heart rate during natural submersion.

The major objectives of the present study were to obtain an estimate of oxygen consumption during natural submersion of tufted ducks and to compare heart rate during submersion with that during surface swimming when oxygen consumption is the same as that during diving. In addition, measurements were made of body temperature and leg movements during surface swimming. The relationship between heart rate and oxygen uptake during transient changes when the ducks were breathing air was investigated.

Some of the results have been briefly presented elsewhere (Butler & Woakes, 1983).

MATERIALS AND METHODS

Six tufted ducks (*Aythya fuligula* L.), that varied in weight from 498–670 g, were used in the experiments. They were raised from eggs obtained from the Wildfowl Trust, Slimbridge and kept in the department's animal house within a wire pen 1·65 × 2·80 m. They had access to a pool 1·5 m in diameter and 30 cm deep. When adult, they were transferred to a deep, glass-sided water tank (1·63 × 1 × 1·7 m deep) with a large (0·60 × 0·80 m) dry area at one corner. The tank is situated in the laboratory where all of the experiments were performed. This allowed the birds to become used to all of the noises and activities associated with the experiments. Mixed grain was thrown onto the water. This encouraged the birds to dive and thus ensured that they had regular exercise.

A pulse interval modulated radiotransmitter (Butler & Woakes, 1982a) was implanted into the abdominal cavity of a bird (for details see Butler & Woakes, 1979) at least 2 weeks before the animal was used in an experiment. The transmitter had a life of 4–5 months. For the first bird used, ECG alone was transmitted, but for the remaining five, deep body temperature was also recorded.

The bird was placed in an experimental area, 0·4 × 1 m, at one end of the tank which was divided from the rest by a sheet of marine-quality plywood coated in polyurethane. The experimental bird could not, therefore, see the others. Although the full volume of the experimental section was available for diving, netting restricted the area into which the bird could surface to 40 cm square. Along two sides of this area there was a ledge 15 cm wide which enabled the duck to leave the water. Long dives were encouraged by the use of an automatic feeder placed on the floor of the tank. The duck soon learnt that a small quantity of mixed grain could be obtained by pressing a coloured lever at the side of the dispenser. By increasing the delay between the operation of this switch and the delivery of the grain, the duration of the dives could be progressively increased as the bird waited, swimming continuously, for the food to appear. The electronic control unit for the feeder also displayed the number of times it had been operated. It was thus possible to ensure that the duck was obtaining an adequate supply of food.

During this period on the experimental section of the tank, the bird was trained to

swim on a variable speed water channel (Armfield Engineering Ltd) which is situated in the same room as the tank. The flume is 6 m long, the test section 0·5 m wide and the depth of water was 0·4 m. Water velocity could be varied between 0 and 1 m s^{-1} and was measured by a Braystoke current flow meter (model BFM 002, Valeport Developments Ltd). The duck swam between two grids of plastic netting placed vertically in the test section, 0·5 m apart and to the full depth of the water. Training lasted for at least 2 weeks, by which time the duck was fully fit and could swim for at least 20 min at any velocity from approximately 0·25 to 0·8 m s^{-1}. During the second week of training an open circuit respirometer (0·4 × 0·4 × 0·2 m deep), constructed from clear acrylic sheet, was placed over the bird. Flexible polythene sheets, placed on the front and near lower edges, provided an airtight seal against the moving water while the side edges projected 5 cm below the water surface. The respirometer was divided by a perforated sheet of acrylic, into two chambers (Fig. 1) with the smaller containing two fans. These ensured that the air in the whole respirometer was mixed in a very short time ($\tau < 1$ s). The bird swam in the larger chamber which measured 0·4 × 0·27 m.

Air was drawn through the respirometer at 10 or 20 l min^{-1}, keeping the concentration of CO_2 in the box below 0·2 % at all times. The difference in the concentration of oxygen in the air entering and leaving the respirometer was measured by a mass spectrometer (Centronics Ltd), thus allowing oxygen uptake of the animal to be calculated (Fig. 1). A rotary valve switched the mass spectrometer gas input from air leaving the respirometer to inlet air for 2 s every 30 s. This allowed any inherent drift in the instrument to be eliminated from the subsequent analysis of the data. Tests showed that there was no detectable loss of O_2 from the system. However, sufficient CO_2 was absorbed by the flowing water to make calculations of CO_2 production inaccurate. They were not, therefore, performed. The signal from the radiotransmitter was passed from a receiver (Sony CRF 5090) to a purpose-built decoder
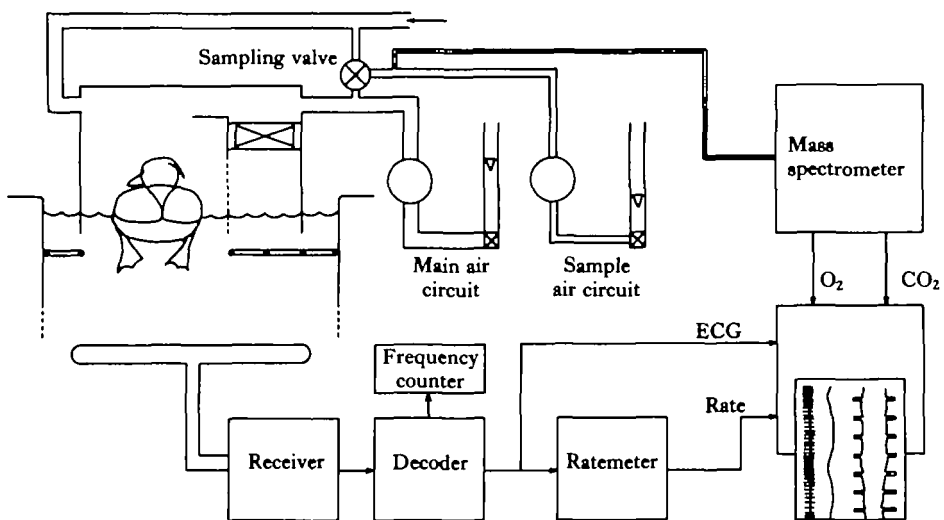

Fig. 1. Diagram of experimental apparatus showing a tufted duck in the respirometer. For further details see Materials and Methods.

(Woakes, 1980), which extracted the ECG. Mean pulse frequency of the transmitted signal varied with deep body temperature of the duck and was monitored by frequency meter (Marconi Instruments). The ECG, instantaneous heart rate and output from the mass spectrometer were recorded on a four-channel, heat-sensitive recorder (Lectromed).

The experimental procedure consisted of swimming the bird at a constant water velocity for at least 20 min, or until the concentration of oxygen in air leaving the respirometer was stable, whichever was the longer. Five minutes after beginning the swimming, ciné film was taken of the leg movements of the duck for subsequent analysis of locomotory variables. The camera (Bolex 16 mm) was set at its maximum nominal frame rate of 64 frames s^{-1} and was calibrated by a light (LED) flashing at exactly 1 Hz within its field of view. At the end of the swimming period, measurements of transmitter pulse frequency, temperatures of air in the respirometer and of the water, and water velocity were taken. Heart rate and oxygen uptake were also obtained at this time. The water velocity was then changed to a new value and the procedure repeated. The water velocities were chosen arbitrarily and the total period of exercise did not exceed 2·5 h. Before and after such a period of exercise, data were recorded from the duck at rest (i.e. no water flow) both with the flume motor on and off. Data were obtained from an average of 44 swimming periods (i.e. of approximately 20 min duration) from each duck, and when this had been completed, the same bird was used to study the energetics of diving on the experimental area of the holding tank.

It is not possible to measure oxygen consumption of a freely diving bird without cannulating air sacs and blood vessels and such procedures could well affect the diving performance of the animal. A technique has been developed, therefore, to estimate the oxygen consumption of an unrestrained, freely diving duck. Feeding activity usually consists of a series of up to 40 closely spaced dives and, because of the tachycardia and hyperventilation present before each dive (Butler & Woakes, 1979), it was assumed that the oxygen stores were fully loaded before each dive. The oxygen uptake of the duck between dives, therefore, represents the amount of oxygen metabolized during the preceding dive plus the amount metabolized at the surface. As there is no correlation between dive duration and the succeeding time at the surface (Butler & Woakes, 1979), a linear multiple regression analysis (Bailey, 1959) between these two variables and oxygen uptake between dives was performed. The regression coefficients represent the mean oxygen consumptions during diving and during the interval between dives, at the mean durations of these activities. Constant factors such as the oxygen used swimming to the bottom of the tank and during surfacing cannot be separately resolved. A similar analysis was applied to CO_2 production as no detectable amount of this gas was absorbed by the water in these experiments.

The open circuit respirometer was used to measure oxygen uptake and carbon dioxide production of the ducks while at rest and during diving activity. The accessible water surface of the experimental area (see earlier) was covered with the respirometer, the lower edges of which projected approximately 5 cm below the water, thus forming a water-tight seal all round. Air was drawn through the box at 10 l min^{-1} and sampled close to the outlet by the mass spectrometer, as previously described. Because of the very good mixing inside the box, the measurements of oxygen and carbon dioxide in the outlet gas were effectively a measure of the mean concentrations

of these gases inside the respirometer. By treating the box as both an open and a closed circuit system and by measuring differences in gas concentrations to within 0·001 %, gas exchange over periods as short as 2 s could be calculated (see Fig. 7), although this was usually done for the complete interdive interval (see Appendix).

The duck was placed in the respirometer box for 6 h each day and recordings were made when it began to perform a series of dives. The acclimation period varied from 0–5 days and approximately 100 dives were recorded from each bird. Diving activity was encouraged by the use of the automatic feeder. Dives that were included for analysis were those where the duck reached the bottom of the tank and which were followed by another within 50 s, thus reducing the possibility of other activity such as preening interfering with the measurements. At the end of longer periods of diving activity, the gas concentrations in the respirometer reached a maximum of 0·35 % for carbon dioxide, and oxygen was reduced by 0·4 % from its ambient level.

Dive duration, duration of the interval before the next dive, and oxygen uptake and carbon dioxide production during that interval were measured for each dive. Mean heart rate during the second half of the dive (see Butler, 1980; Butler & Woakes, 1979) was also recorded. Oxygen consumptions and carbon dioxide productions for each bird were then calculated as described earlier. All gas volumes are corrected to STPD.

Generally, mean values for a variable were obtained for each duck. These mean values were then averaged and the standard error (S.E.) of this final mean obtained. Thus, in these cases the number of observations (N) was 6. On occasion, the quoted mean value is that obtained from the total number of observations from all ducks, in which case $N > 6$. Student's t test or, when appropriate, the method of paired comparisons were used to test the significance of any difference between two mean values and the word 'significant' in the present report means at the 95 % confidence level ($P < 0·05$).

RESULTS

Swimming

There were small but insignificant increases in resting heart rate and oxygen uptake when the motor of the water channel was switched on (Table 1). When referring to factorial changes in a variable relative to the resting value, it is with respect to the value recorded with the motor turned off. In all six ducks, heart rate and oxygen uptake changed little up to a swimming velocity of 0·5–0·6 m s^{-1}, when there was a large increase in each (Fig. 2A,B). At an average velocity of 0·4 m s^{-1}, oxygen uptake was significantly (10 %) greater than that measured at rest with the motor on and 17 % greater than at rest with the motor off. For each duck there was a good linear relationship between heart rate and oxygen uptake (Fig. 3), with the correlation coefficient (r) for each regression equation varying between 0·91 and 0·96. For all six ducks the equation for the relationship was $y = (64·7 \pm 4·3) + (285 \pm 27)\chi$, where y = heart rate in beats min^{-1}, χ = oxygen uptake in ml s^{-1} STPD and $r = 0·935 \pm 0·007$. At the highest average sustainable swimming speed (0·78 $\pm$ 0·014 m s^{-1}) heart rate was two times resting and oxygen uptake was 3·81 times resting.

Deep body temperature (T_B) decreased significantly at the lower swimming

Table 1. *Mean values (± S.E.) of measured variables in six tufted ducks at rest and while swimming on a water channel at various velocities*

	Rest			Swimming		
	Motor off	Motor on				
Velocity (m s^{-1})	0	0	0·25	0·4		0·78
Oxygen consumption (ml s^{-1} STPD)	0·168 ± 0·011	0·179 ± 0·011	–	0·197 ± 0·006(25)		0·64 ± 0·02
Heart rate (beats min^{-1})	117 ± 8·2	122 ± 8·7	–	125 ± 5·4(25)		235 ± 12·4
Deep body temperature (°C)	41·38 ± 0·09(63)	–		–	40·86 ± 0·12(32)	42·34 ± 0·07(5)
Leg beat frequency* (beats min^{-1})	–	–	133	–		210
Leg beat amplitude* (cm)	–	–	8·6	–		13·6
Water temperature (°C)	17·79 ± 0·38					
Body mass (g)	613 ± 27					

* Taken from linear regression equations in Fig. 5.
Resting values were obtained with the motor of the channel turned off and with it on. Number of observations is six except where number is given in parentheses (see Materials and Methods).

velocities, while oxygen uptake was still close to the resting value (Table 1, Fig. 4). As oxygen uptake increased above 0·2 ml O$_2$ s^{-1}, T$_B$ increased to approximately 41·8 °C and only at the highest oxygen uptake did T$_B$ rise significantly above this level (Table 1, Fig. 4).

Both leg beat frequency and leg beat amplitude (measured as excursion of tip of foot) increased linearly with swimming velocity, and at the highest swimming velocity both these variables were 58 % greater than at the lowest velocity (Table 1, Fig. 5A, B). Mean foot velocity increased from 0·39 m s^{-1} to 1·07 m s^{-1} over the same range of swimming speeds. The power stroke occupied, on average, 44 % of the total leg beat cycle, and this was independent of swimming velocity (Fig. 5C).

Diving

When resting on the experimental section of the water tank, heart rate was 9 %, but not significantly, lower than it was on the water channel with the motor turned off, whereas oxygen uptake was almost identical (Tables 1, 2). *Total* oxygen uptake and CO$_2$ production between dives were 16·2 ± 2·3 ml and 14·8 ± 2·6 ml respectively and respiratory quotient (RQ) was 0·9 ± 0·026. Of these totals, the amounts of oxygen metabolized and CO$_2$ produced at mean dive duration and at mean interdive period
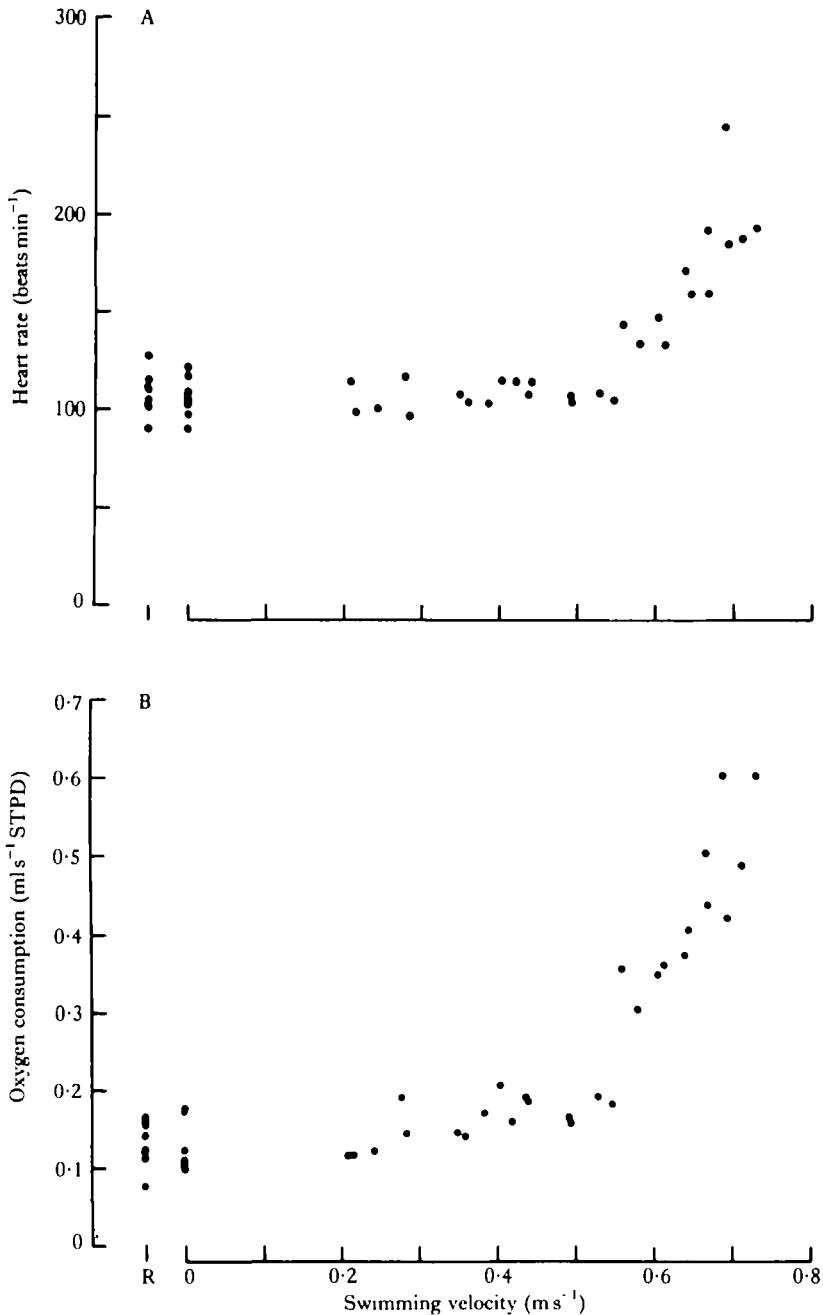
Fig. 2. (A) Heart rate and (B) oxygen consumption of ♂ tufted duck of mean mass (±s.e.) 503 ± 5·8 g at different swimming velocities. R, rest with motor of water tunnel turned off. At 0 m s⁻¹, motor of water tunnel turned on.

are given in Table 2. These values were obtained by multiple regression analysis as described in the Materials and Methods section. For each duck the relevant values for oxygen consumption and carbon dioxide production were closely related to dive
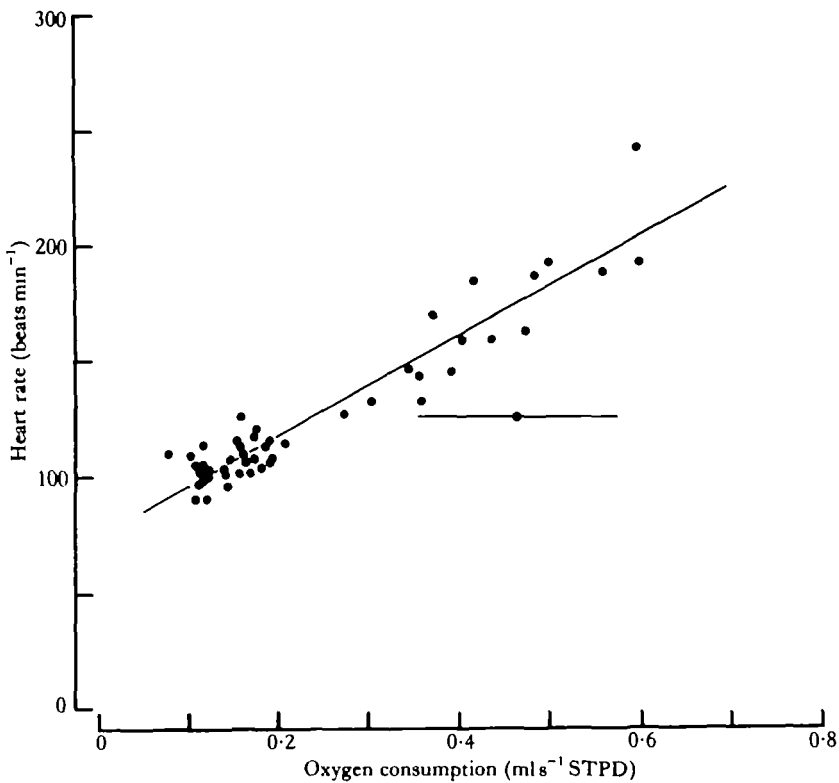
Fig. 3. Relationship between heart rate and oxygen uptake of ♂ tufted duck (the same as in Fig. 2) while swimming at different velocities. The point with the horizontal bar is mean oxygen consumption (±s.E.) and mean heart rate at mean dive duration of the same bird.

Table 2. *Mean (± s.E.) of measured variables in six tufted ducks (the same as those in Table 1) at rest and during diving activity on a 1·7 m deep water tank*

	Rest	Anticipation period before 1st dive of series	Dives	Between dives
Heart rate (beats min⁻¹)	106 ± 3·9	326 ± 13·9(19)	160 ± 14·8	–
Oxygen consumption (ml s⁻¹ STPD)	0·163 ± 0·006	1·031 ± 0·082(24)	0·566 ± 0·05	0·444 ± 0·073
CO_2 production (ml s⁻¹ STPD)	0·144 ± 0·005	1·031 ± 0·098(24)	0·502 ± 0·04	0·476 ± 0·097
RQ	0·84 ± 0·028	1·04 ± 0·065(24)	0·90 ± 0·036	1·051 ± 0·042
Duration (s)	–	6·8 ± 0·77	14·4 ± 1·86	16·12 ± 2·53
Water temperature (°C)	13·64 ± 1·65			
Mass (g)	597 ± 26			

Number of observations is six except where number is given in parentheses (see Materials and Methods).
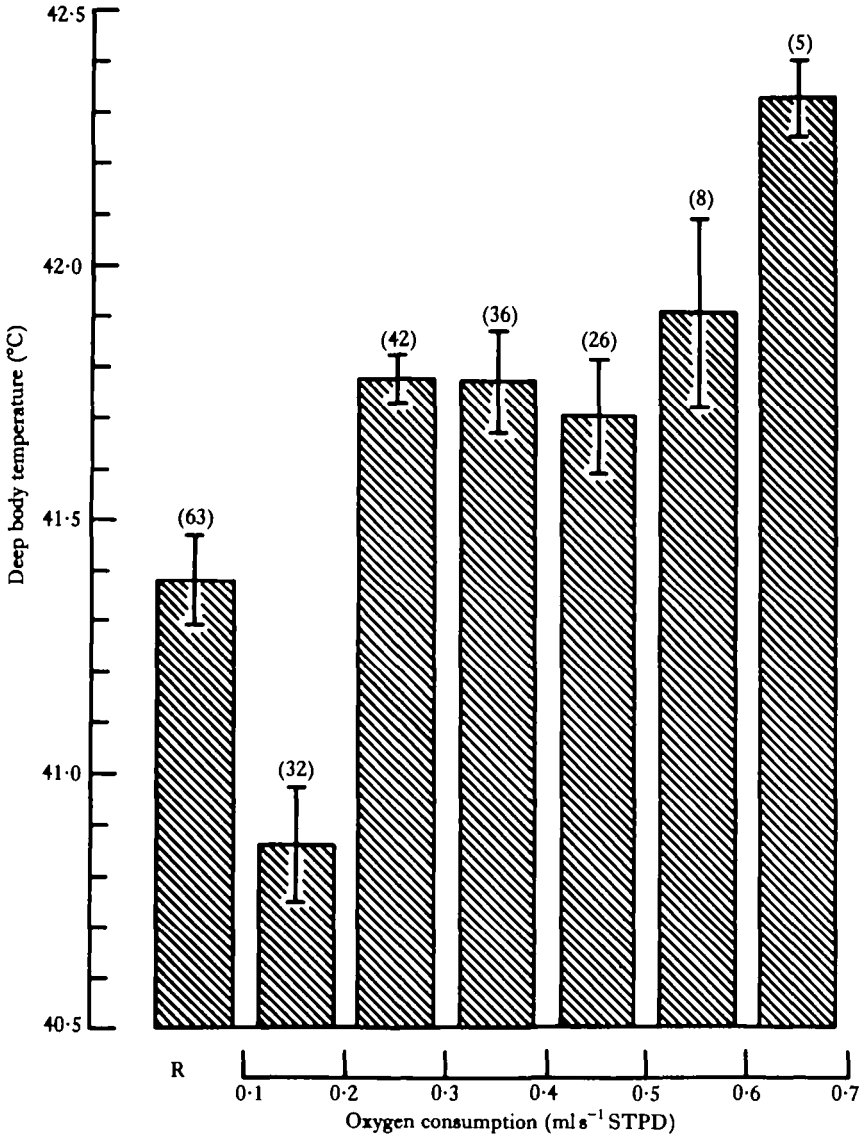
Fig. 4. Mean values of deep body temperature from six tufted ducks at rest on the water channel (R) and at different values of oxygen consumption while swimming. Number of observations is given in parentheses above each histogram. Mean water temperature was $17.79 \pm 0.38\,°C$.

duration and interdive interval. During the dives, calculated oxygen consumption ranged from 0.38 ± 0.064 ($N = 57$) to 0.68 ± 0.07 ($N = 94$) ml s^{-1}, with partial correlation coefficients ranging from 0.57 to 0.79 (mean 0.695 ± 0.030). Carbon dioxide production ranged from 0.39 ± 0.098 to 0.61 ± 0.092 ml s^{-1} (the same birds as for oxygen consumption) with partial correlation coefficients ranging from 0.52 to 0.79 (mean 0.657 ± 0.041). During the intervals, the corresponding values were 0.33 ± 0.025 ($N = 73$) to 0.81 ± 0.057 ($N = 88$) ml s^{-1} for oxygen consumption with partial
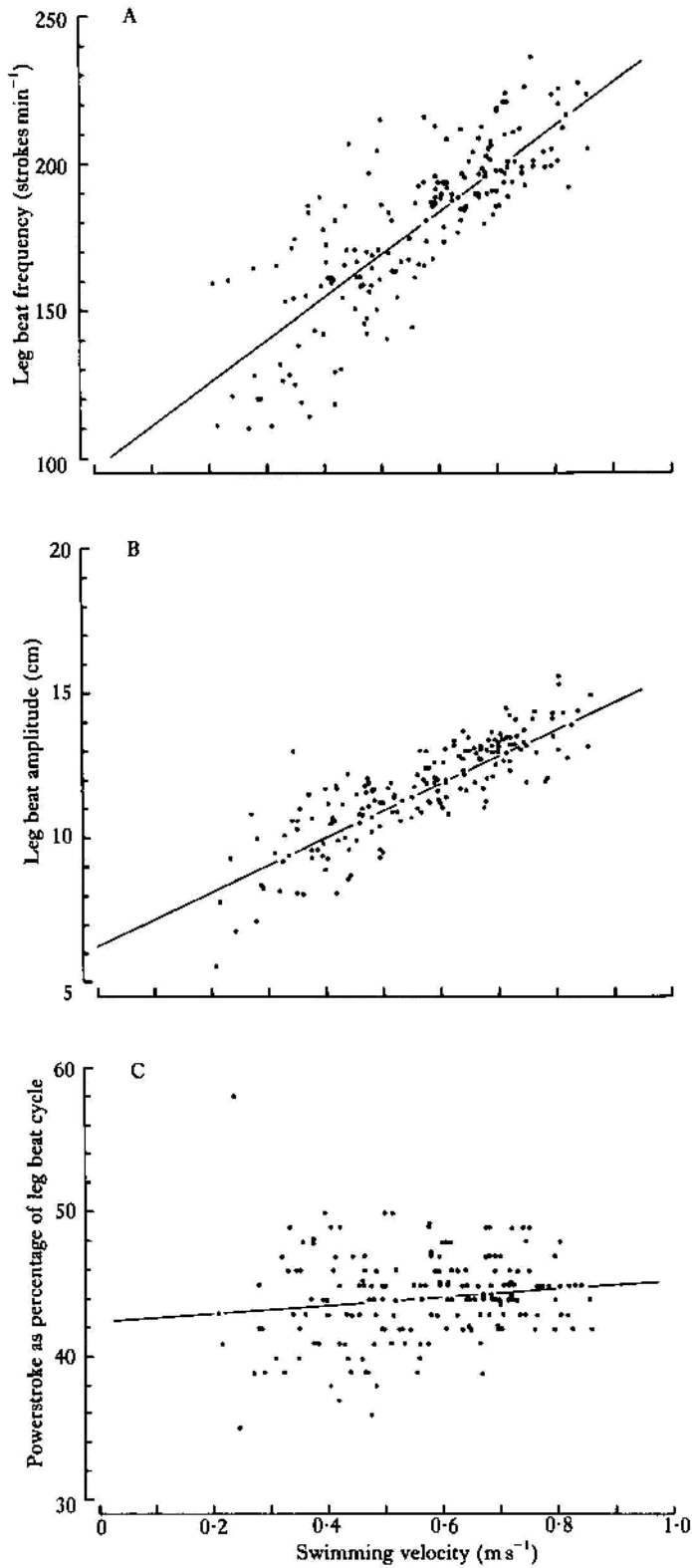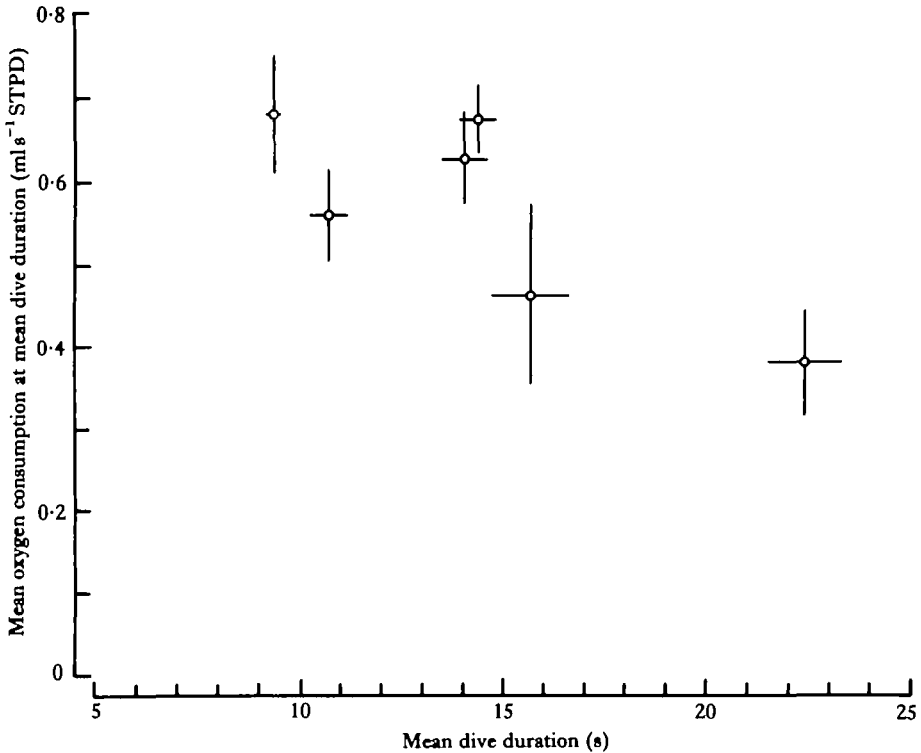
Figs 5A–C

Fig. 6. Relationship between mean oxygen consumption ($\pm$s.e.) at mean dive duration and mean dive duration ($\pm$s.e.) for six tufted ducks.

correlation coefficients from 0·60 to 0·90 (mean 0·756 $\pm$ 0·041), and 0·35 $\pm$ 0·023 ($N = 94$) to 0·96 $\pm$ 0·083 ($N = 88$) ml s^{-1} for carbon dioxide production, with partial correlation coefficients from 0·65 to 0·87 (mean 0·757 $\pm$ 0·037).

At the mean dive duration of 14·4 s, oxygen consumption was 3·47 times the resting value and CO_2 production was 3·49 times resting. There was, therefore no significant change in the RQ from the resting value (Table 2). Oxygen consumption was not significantly different from that at maximum sustainable swimming velocity (see Table 1). Heart rate during the latter stages of the dives was 51 % higher than the resting value. At the mean interdive duration of 16·1 s, oxygen consumption was 2·7 times the resting value whereas CO_2 production was 3·3 times resting, giving a significant increase in RQ.

Mean dive duration was different for each duck, varying between 9·4 $\pm$ 2·2 to 22·4 $\pm$ 0·9 s, and mean oxygen consumption tended to be lower in the ducks with the longer mean dive duration (Fig. 6). Although the overall trend was not statistically significant, oxygen consumption during submersion was significantly (44 %) lower in

Fig. 5. Regression lines of (A) leg beat frequency, (B) leg beat amplitude and (C) percentage of leg beat cycle occupied by power stroke against swimming velocity in six tufted ducks. Equations describing regression lines are (A) $y = 96\cdot48 + (145\cdot05 \pm 8\cdot08)\chi$, $r = 0\cdot81$; (B) $y = 6\cdot29 + (9\cdot35 \pm 0\cdot59)\chi$, $r = 0\cdot76$; (C) $y = 42\cdot5 + (2\cdot9 \pm 1\cdot5)\chi$, $r = 0\cdot15$.

the duck that performed the longest dives than in that which dived for the shortest duration.

For each duck, mean oxygen consumption and mean heart rate at average dive duration were plotted on the heart rate/oxygen uptake curve obtained from the swimming experiments and heart rates at the same level of oxygen consumption were compared (see Fig. 3). In all cases, heart rate was lower during diving. The difference between the two values varied from 24 to 112 beats min^{-1} between birds and was, on average, $59 \pm 14 \cdot 9$ beats min^{-1}. This is significantly different from zero. For all ducks, at the oxygen uptake calculated during diving (mean value of $0 \cdot 566$ ml s^{-1}), mean heart rate was $219 \pm 21 \cdot 2$ beats min^{-1} while swimming on the channel and $160 \pm 14 \cdot 8$ beats min^{-1} at average dive duration.

Associated with the tachycardia and increased respiratory frequency before the first dive of a series (Butler & Woakes, 1979; Butler, 1980) there were substantial increases in oxygen uptake and CO_2 output (Table 2) to $6 \cdot 3$ and $7 \cdot 2$ times resting, respectively. Fig. 7 shows instantaneous heart rate and gas exchange for one particular bird that often exhibited the 'anticipatory' changes that precede a dive without subsequently
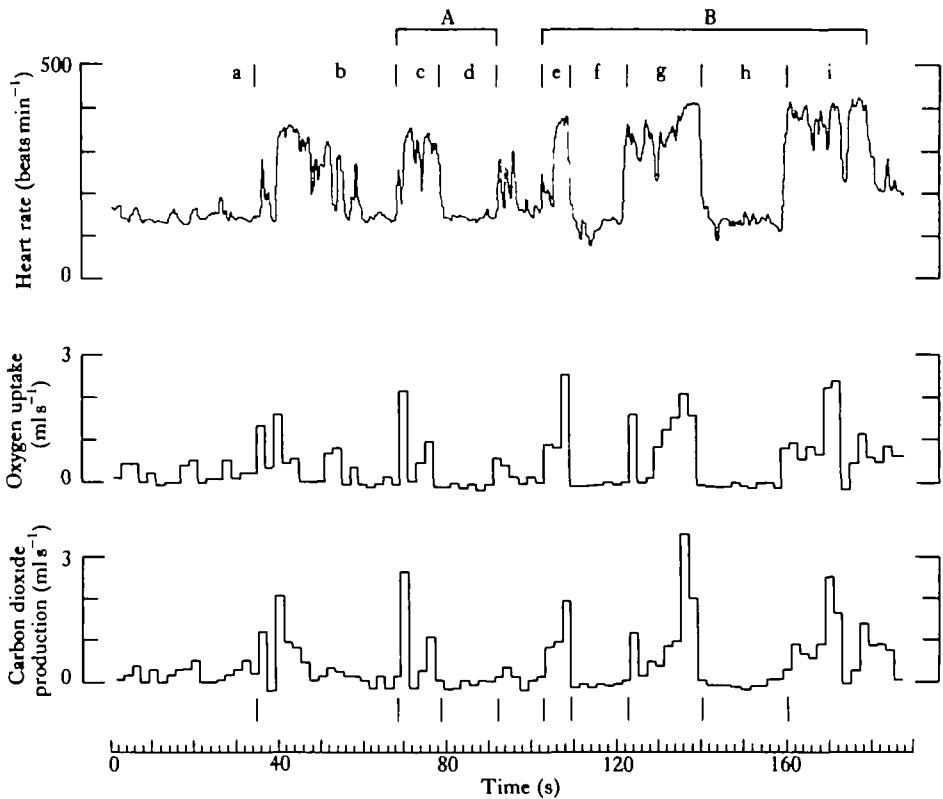

Fig. 7. Relationship between instantaneous heart rate and gas exchange (calculated over 2-s intervals) in ♂ tufted duck (580 g) during a 'pseudo'-dive (A), when anticipatory changes in heart rate and gas exchange occur but no dive follows, and during two subsequent voluntary dives (B). The sections a–i are labelled merely for identification in the text.

diving. During the anticipatory period (c), mean oxygen uptake was $0.91 \, \mathrm{ml \, s^{-1}}$ compared with $1.41 \, \mathrm{ml \, s^{-1}}$ for a period preceding a true dive (e). Despite the fact that the animal remained at the surface after (c), gas exchange fell to zero as heart rate returned to the 'pre-elevation' level (d). During, and particularly at the end of the preceding active period (b), there are further, but less evident, examples of this behaviour. The short intervals of no gas exchange during rest (a) are, most probably, related to the low respiratory frequency of the bird (gas exchange being measured over 2-s intervals) and are at least 50 % shorter in duration than period (d).

DISCUSSION

The energetics of swimming in ducks has already been studied in detail by Prange & Schmidt-Nielsen (1970) and in many respects our results are in agreement with theirs. Their paper should be consulted for a discussion of these results. There are, however, one or two discrepancies which are worthy of mention.

Our tufted ducks at rest on the water channel with the motor switched off had an oxygen consumption of $0.99 \, \mathrm{l \, kg^{-1} \, h^{-1}}$, which is very similar to the value recorded by Prange & Schmidt-Nielsen (1970) for mallard ducks at rest in a dry chamber. These authors found that when their ducks were resting on water, oxygen uptake was 38 % higher than when they were in air. This could have been the result of heat loss to the water. At low swimming velocities (0.25–$0.55 \, \mathrm{m \, s^{-1}}$), oxygen uptake was 64 % higher than when the ducks were resting in water (i.e. twice the resting in air values). In the present experiments, however, oxygen uptake was only 17 % higher than the value recorded when the birds were resting on the water channel with the motor off. The explanation for this difference is not immediately obvious. It could be that our ducks 'diverted' some of the energy that was being used to maintain body temperature when at rest on water to the leg muscles during swimming, whereas this was not done, or at least not to such a great extent, by the ducks used by Prange & Schmidt-Nielsen (1970). Certainly, water temperature was about $5\,^{\circ}\mathrm{C}$ lower in the present experiments, and body temperature fell by approximately $0.5\,^{\circ}\mathrm{C}$ below the resting value at the lower swimming velocities. Of course, the lower oxygen consumption by the tufted ducks at the lower swimming velocities, means that their cost of transport ($3.48 \, \mathrm{kcal \, kg^{-1} \, km^{-1}}$ at $0.5 \, \mathrm{m \, s^{-1}}$) was lower than that measured by Prange & Schmidt-Nielsen (1970) for mallards ($5.77 \, \mathrm{kcal \, kg^{-1} \, km^{-1}}$ at $0.5 \, \mathrm{m \, s^{-1}}$).

Our ducks, in contrast to those of Prange & Schmidt-Nielsen (1970), did not exhibit a constant leg beat frequency at different swimming velocities and no explanation can be offered for this discrepancy. When swimming at a mean velocity of $0.63 \, \mathrm{m \, s^{-1}}$, leg beat frequency of the tufted ducks was similar to that measured from one duck feeding on the bottom of a water-filled tank (Butler & Woakes, 1982a).

Our data are in complete agreement with those of Bamford & Maloiy (1980) which demonstrated that during steady state exercise, heart rate is a good indicator of oxygen consumption. This relationship cannot, however, be used to predict oxygen uptake from heart rate during natural diving nor, it would seem, during large transient changes when breathing air. If, from the present data, heart rate at mean dive duration is used to calculate oxygen consumption during diving from the heart rate/oxygen consumption relationship during swimming, the value for oxygen uptake during

diving is, on average, 42 % less than that measured more directly by respirometry. Also, oxygen uptake may fall to zero following a brief period of enhanced gas exchange if there is no increased activity, but heart rate returns to a value close to its resting level (see Fig. 7). A similar phenomenon has been described in pigeons while panting after flying for 10 min or more in a wind tunnel (Butler, West & Jones, 1977) and clearly deserves further study.

As already indicated, the method used to determine gas exchange gives the mean values of oxygen consumption and carbon dioxide production at the average duration of the dives. It does not, therefore, take into account the extra energy involved in getting to the bottom, although this may be counterbalanced, to a certain extent at least, by the fact that surfacing is purely passive and that the durations of descent and ascent are similar (Butler & Woakes, 1982a). Neither does it allow oxygen consumption for an individual bird to be determined as the dive progresses, when presumably the bird becomes less buoyant as a result of the loss of air from beneath the feathers (Butler & Woakes, 1982a). Nonetheless there is no doubt that, contrary to what happens during forced submersion and to what was thought to happen during natural dives, there is a substantial increase in oxygen consumption, above the resting level, during spontaneous dives. In fact, oxygen consumption during underwater swimming is similar to that recorded at maximum sustainable swimming velocity at the surface.

It is almost impossible to make useful comparisons between these data and those obtained for Weddell seals (Kooyman, Kerem, Campbell & Wright, 1973) and king penguins (Kooyman, Davis, Croxall & Costa, 1982) during foraging (diving). The seals and penguins were in cold antarctic water which, for the penguins at least (Kooyman, Gentry, Bergman & Hammel, 1976), probably raises their metabolic rate substantially above the true resting value (see Butler & Jones, 1982). Also, seals and penguins are better adapted than ducks to underwater locomotion. One laboratory study on harbour seals (Craig & Påsche, 1980) indicates that oxygen consumption during spontaneous diving is approximately 65 % greater than during inactivity. This is qualitatively similar to the present findings in ducks.

It is suggested that the circulatory adjustments during diving in ducks are similar to those during exercise in air in as much as the locomotory muscles (as well as the heart and CNS) receive an enhanced blood supply and the inactive muscles, viscera and kidneys receive a reduced supply (see Butler, 1982). The lower heart rate during diving could indicate, however, that the selective vasoconstriction is more intense and that the oxygen extraction by the active muscles is greater when the ducks exercise under water and are thus apnoeic, than when they exercise in air (Butler, 1982). Certainly the respiratory muscles are inactive when under water, unlike the situation during exercise in air, and probably receive a reduced blood supply. Heart rate is higher at the end of relatively long (>20 s) natural dives after denervation of the carotid bodies (Butler & Woakes, 1982b); this also suggests that in intact ducks during voluntary dives there is partial expression of the cardiovascular adjustments that are seen during forced submersion. During voluntary diving there would appear to be a balance between the cardiovascular responses to forced submersion and to exercise in air, with the bias towards the latter (Fig. 8).

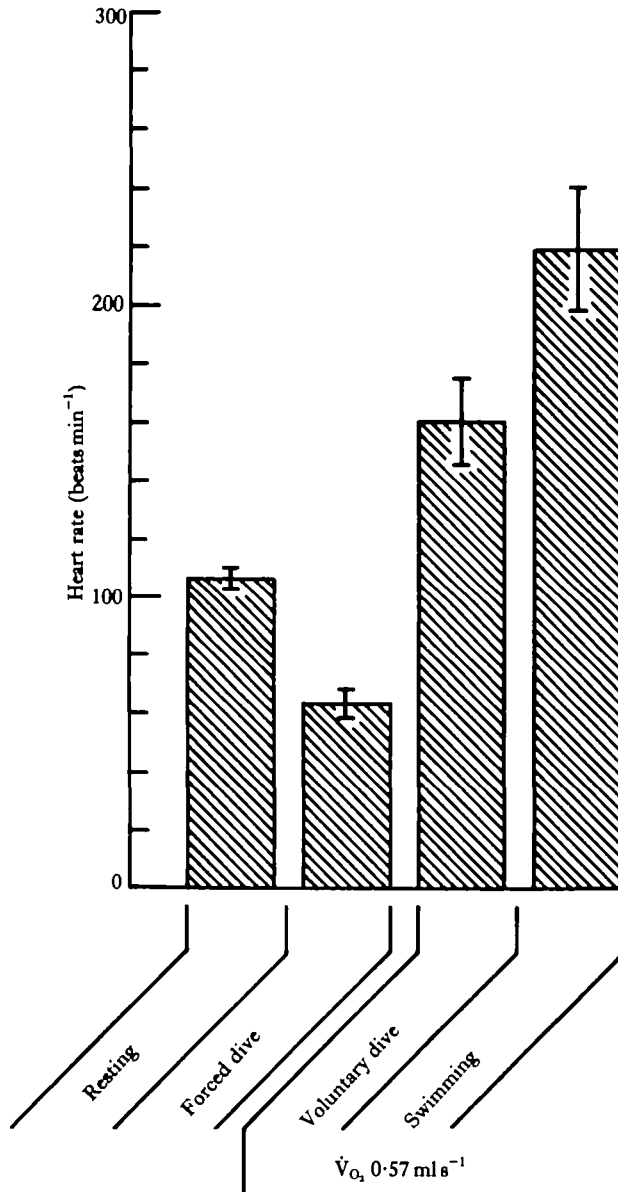From the present estimate of oxygen consumption during diving and the value of

Fig. 8. Mean heart rate (±s.e.) for six tufted ducks (except during forced dive where 10 ducks were used) at rest, 15 s after forced submersion of head (from Butler & Woakes, 1982b), during voluntary dives of 14·4 s mean duration and while swimming. Oxygen consumption ($\dot{V}_{O_2}$) at mean dive duration and while swimming was the same – 0·57 ml s^{-1} (see text for further details).

usable oxygen stores in tufted ducks (Keijer & Butler, 1982), aerobic metabolism could continue for 44 s with the duck actively swimming under water. This is close to the previous estimate by Butler & Woakes (1982a) and indicates that animals in the present experiments and those in the wild diving to depths of 6 m (Draulans, 1982) surfaced, on average, with plenty of available oxygen still present in their bodies. There is no reason to doubt, therefore, that like Weddell seals (Kooyman et al. 1980),

the majority of dives of tufted ducks are completely aerobic with the animals merely replacing their oxygen stores between dives.

It is also clear that the hyperventilation and tachycardia preceding the first dive of a series (Butler & Woakes, 1979; Butler, 1980) serve to load the oxygen stores before a bout of diving commences. The increased activity of the respiratory muscles during this period no doubt raises oxygen consumption above the resting level. Even assuming, at the extreme, that oxygen consumption is similar to that calculated for the average duration between dives, an extra 4 ml of O_2 is taken in by the ducks during the anticipation period before the first dive of a series. This would allow the animals to remain under water and metabolize aerobically for an extra 7 s (i.e. for a total of 51 s). The excessive removal of carbon dioxide during the anticipation period before a series of dives will, no doubt, reduce the stimulatory influences on the respiratory system (Butler, 1982). This could, at least partly, explain why in one bird gas exchange ceased following a period of anticipatory tachycardia and hyperventilation with no subsequent dive. In terms of gas exchange, the bird behaved just as if it did dive. Unfortunately it is not known whether or not the bird was apnoeic during the 'post-anticipatory' period.

In conclusion, in contrast to the situation during forced dives, both oxygen consumption and heart rate increase above the resting level during natural submersion of tufted ducks. Heart rate is, however, lower than would be predicted from the oxygen uptake/heart rate relationship obtained from ducks swimming on a water channel. It is suggested that during natural diving in ducks there is, in effect, a balance between the cardiovascular responses to forced submersion and to exercise in air (cf. Millard, Johansen & Milsom, 1973), with the bias toward the latter.

APPENDIX

An open circuit respirometer system is not capable of measuring fast changes in oxygen uptake and carbon dioxide production. A technique has been developed that allows such a system, with the minor modifications noted in the Methods section, to make such measurements over periods as short as 2 s, while still retaining its advantages of large animal space, and small excursions of gas concentrations from their atmospheric values.

Consider the variation of the concentration of a gas (say carbon dioxide, Fig. 9A) in the respirometer over a period of time, t_1 to t_2. Let the fractional concentration of this gas be C_1 at t_1 and change to C_2 at time t_2. The gases within the respirometer (of volume V) are assumed to be fully mixed, and C_1 and C_2 are measured relative to the ambient atmospheric value. This change in gas concentration is caused by the difference between the carbon dioxide produced by the bird and that flushed out by the fixed flow, $\dot{Q}$, through the respirometer. Quantifying the amount of gas removed from the respirometer, and the change in the amount of carbon dioxide left within the respirometer enables the gas production of the bird to be measured, and is equal to the sum of these two terms. As the contents of the respirometer are well mixed, it can be assumed that the concentration measured at the outlet is identical to that within the respirometer.

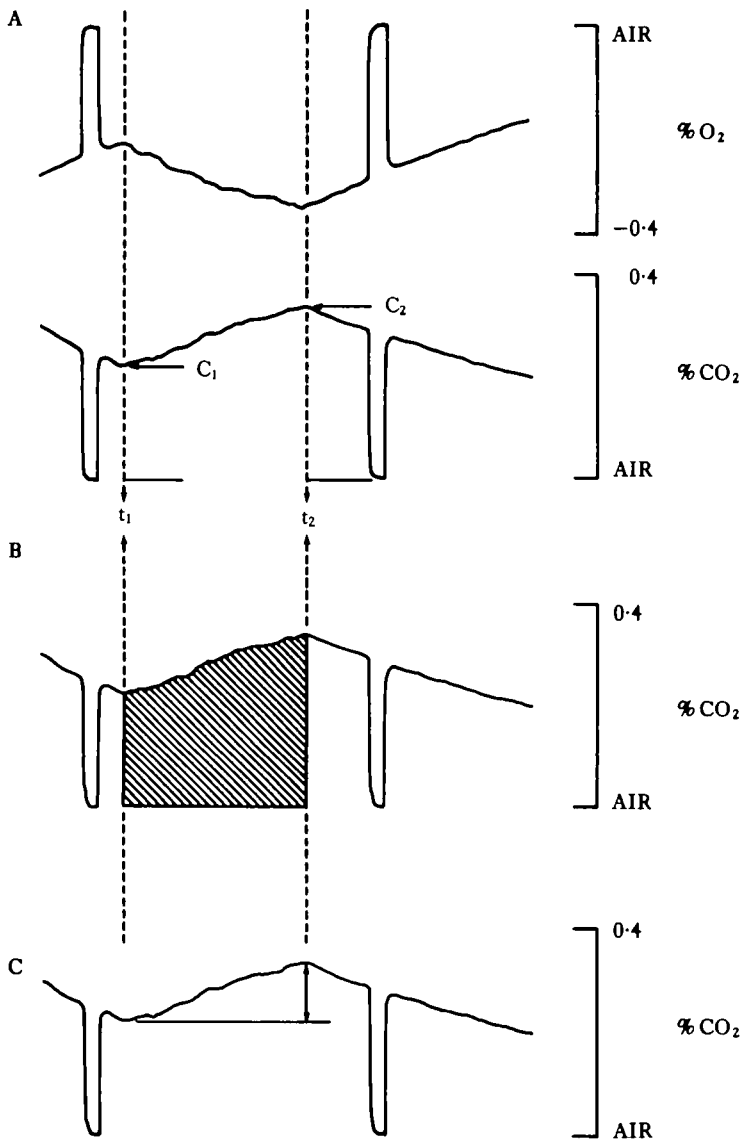The carbon dioxide removed from the respirometer in the period t_1 to t_2 is given by

Fig. 9. (A) Diagrams to illustrate changes in concentration of oxygen and carbon dioxide in the respirometer while duck at the surface (S) and during a voluntary dive (D). (B, C) Diagrams to illustrate measurements taken from CO_2 trace for calculation of CO_2 production of duck while at the surface (for details, see text).

$$\int_{t_2}^{t_3} C dt \dot{Q} \qquad\qquad \text{(Fig. 9B)}$$

If the concentration varies linearly over the time period, the term can be simplified to:

$$\frac{[C_1 + C_2]}{2} [t_2 - t_1] \dot{Q}.$$

The change in the amount of carbon dioxide within the respirometer is given by:

$$[C_2 - C_1] V \qquad\qquad \text{(Fig. 9C)}$$

and this term can be of either sign.

Therefore the amount of carbon dioxide produced by the bird in the given time interval is:

$$[C_2 - C_1]V + \frac{[C_1 + C_2]}{2}[t_2 - t_1]\dot{Q}$$

and an equivalent analysis may be applied to oxygen uptake.

The oxygen uptake and carbon dioxide production over a given period can therefore be calculated from measurements of the fractional concentrations of these gases at the beginning and end of this period. In this paper, the period taken is that of the inter-dive interval, which varied from 5 to 50 s. The analysis may be applied to longer periods, but care should be taken that the approximation for the integral term is not invalid. If the concentration does not vary linearly from C_1 to C_2 then it is probable that the period can be subdivided into shorter intervals to improve the approximation. For short periods, the volume term dominates the analysis, and the instrument noise in measuring the fractional concentrations produces increasingly large errors. The mass spectrometer used in this study (Centronics, MGA 007) was optimized for low noise, and further filtering reduced the RMS noise level to 0·003 % for oxygen, and 0·001 % for carbon dioxide (expressed as equivalent % gas concentrations). Signal averaging reduced the error in measurement of both gases to 0·001 %. Periods as short as 2 s could be analysed (Fig. 7) with an error of approximately ±0·3 ml. As the period is extended, this absolute error remains constant, but becomes an increasingly smaller percentage of the total gas uptake or production. This error can be reduced either by improving the instrument noise figure or by reducing the respirometer volume. Errors due to baseline drift of the instrument were removed by automatically sampling the ambient air for 2 s every 30 s. Gain drift was monitored by fully calibrating the system before and after each experiment, and was found to be negligible.

REFERENCES

BAILEY, N. T. J. (1959). *Statistical Methods in Biology*. London: The English Universities Press Ltd.

BAMFORD, O. S. & MALOIY, G. M. O. (1980). Energy metabolism and heart rate during treadmill exercise in the Marabou stork. *J. appl. Physiol.* 49, 491–496.

BUTLER, P. J. (1980). The use of radio telemetry in the studies of diving and flying of birds. In *A Handbook of Biotelemetry and Radio Tracking*, (eds C. J. Amlaner Jr. & D. W. Macdonald), pp. 569–577. Oxford: Pergamon.

BUTLER, P. J. (1982). Respiratory and cardiovascular control during diving in birds and mammals. *J. exp. Biol.* 100, 195–221.

BUTLER, P. J. & JONES, D. R. (1982). Comparative physiology of diving in vertebrates. In *Advances in Physiology and Biochemistry*, Vol. 8, (ed. O. E. Lowenstein), pp. 179–364. New York: Academic Press.

BUTLER, P. J., WEST, N. H. & JONES, D. R. (1977). Respiratory and cardiovascular responses of the pigeon to sustained, level flight in a wind-tunnel. *J. exp. Biol.* 71, 7–26.

BUTLER, P. J. & WOAKES, A. J. (1976). Changes in heart rate and respiratory frequency associated with natural submersion in ducks. *J. Physiol., Lond.* 256, 73–74P.

BUTLER, P. J. & WOAKES, A. J. (1979). Changes in heart rate and respiratory frequency during natural behaviour of ducks, with particular reference to diving. *J. exp. Biol.* **79**, 283–300.

BUTLER, P. J. & WOAKES, A. J. (1982a). Telemetry of physiological variables from diving and flying birds. *Symp. Zool. Soc. Lond.* **49**, 106–128.

BUTLER, P. J. & WOAKES, A. J. (1982b). Control of heart rate by carotid body chemoreceptors during diving in tufted ducks. *J. appl. Physiol.* **53**, 1405–1410.

BUTLER, P. J. & WOAKES, A. J. (1983). Heart rate and oxygen uptake in tufted ducks, *Aythya fuligula*, during swimming and spontaneous diving. *J. Physiol., Lond.* **338**, 55–56P.

CRAIG, A. B. & PÅSCHE, A. (1980). Respiratory physiology of freely diving harbor seals (*Phoca vitulina*). *Physiol. Zool.* **53**, 419–432.

DRAULANS, D. (1982). Foraging and size selection of mussels by the tufted duck, *Aythya fuligula*. *J. Anim. Ecol.* **51**, 943–956.

KEIJER, E. & BUTLER, P. J. (1982). Volumes of the respiratory and circulatory systems in tufted and mallard ducks. *J. exp. Biol.* **101**, 213–220.

KOOYMAN, G. L., KEREM, D. H., CAMPBELL, W. B. & WRIGHT, J. J. (1973). Pulmonary gas exchange in freely diving Weddell seals. *Respir. Physiol.* **17**, 283–290.

KOOYMAN, G. L., GENTRY, R. L., BERGMAN, W. P. & HAMMEL, H. T. (1976). Heat loss in penguins during immersion and compression. *Comp. Biochem. Physiol.* **54A**, 75–80.

KOOYMAN, G. L., WAHRENBROCK, E. A., CASTELLINI, M. A., DAVIS, R. W. & SINNETT, E. E. (1980). Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behaviour. *J. comp. Physiol. B.* **138**, 335–346.

KOOYMAN, G. L., DAVIS, R. W., CROXALL, J. P. & COSTA, D. P. (1982). Diving depths and energy requirements of king penguins. *Science, N.Y.* **217**, 726–727.

MILLARD, R. W., JOHANSEN, K. & MILSOM, W. K. (1973). Radiotelemetry of cardiovascular responses to exercise and diving in penguins. *Comp. Biochem. Physiol.* **46A**, 227–240.

PRANGE, H. D. & SCHMIDT-NIELSEN, K. (1970). The metabolic cost of swimming in ducks. *J. exp. Biol.* **53**, 763–777.

WOAKES, A. J. (1980). *Biotelemetry and its Application to the Study of Avian Physiology*. Ph.D. thesis: Birmingham University.