J. exp. Biol. **126**, *341–359 (1986)*
Printed in Great Britain © The Company of Biologists Limited 1986

DIVING BEHAVIOUR AND HEART RATE IN TUFTED DUCKS (*AYTHYA FULIGULA*)

BY R. STEPHENSON, P. J. BUTLER AND A. J. WOAKES

Department of Zoology and Comparative Physiology, The University of Birmingham, PO Box 363, Birmingham B15 2TT, UK

Accepted 23 July 1986

SUMMARY

Diving behaviour and heart rate were monitored in tufted ducks diving under circumstances which simulated various environmental conditions such as feeding under ice in winter.

When distance to food was increased on a covered outdoor pond, dive duration increased proportionately, but it was calculated that time available for feeding was reduced during the longer-distance 'extended' dives. There was a gradual reduction in heart rate to 77·3 ± 13·8 beats $\min^{-1}$, which is significantly lower than the resting value of 121·1 ± 14·1 beats $\min^{-1}$, during the course of extended dives, suggesting that the ducks could gradually switch over to a 'classical' oxygen-conserving response during these prolonged voluntary dives. The duration of the pre-dive preparatory period was positively correlated with dive distance.

When the ducks were briefly unable to resurface during an otherwise normal feeding dive in an indoor tank, a situation which may occur if they become disoriented under ice, there was an immediate switch to a full bradycardia. Reduction in heart rate during these 'enclosed' dives occurred only when the ducks were apparently aware of the situation and the rate of onset of bradycardia was very similar to that previously observed during involuntary submersion of tufted ducks. Minimum heart rate was the same at 46 beats $\min^{-1}$ after 15 s of enclosed dives and after 30 s of involuntary submersions, despite the differences in levels of activity in the two situations.

INTRODUCTION

It has been repeatedly demonstrated that an orchestrated set of cardiovascular adjustments occurs in birds and mammals in response to involuntary submersion in water (e.g. Scholander, 1940; Butler & Jones, 1982). It is generally believed that these adjustments function to conserve endogenous oxygen stores for the use of those tissues which cannot withstand periods of oxygen depletion, principally the central nervous system and heart (Irving, 1934, 1939). Oxygen conservation is effected through a selective peripheral vasoconstriction with anaerobiosis (and, therefore, accumulation of lactic acid) in the underperfused tissues. This is accompanied by a reduction in cardiac output (Jones *et al.* 1979; Blix, Elsner & Kjekshus, 1983) which

Key words: diving, bradycardia, behaviour, ducks.

results almost entirely from a fall in heart rate, the so-called 'diving bradycardia'. The presence of a bradycardia is often taken, either implicitly or explicitly, as an indication of the occurrence of the other physiological and metabolic adjustments (e.g. Blix & Folkow, 1983; Gabrielsen, 1985).

Observations of natural diving behaviour have shown that the vast majority of dives in all aquatic birds and mammals are of shorter duration than the maximum endurance times which have been demonstrated in restrained animals (Kooyman, Drabek, Elsner & Campbell, 1971; Kooyman *et al.* 1980). Furthermore, natural dives usually occur in series, one dive being closely followed by another with only a very brief recovery period between the two (Dewar, 1924; Butler & Woakes, 1979).

On the basis of measured oxygen storage capacities and estimated rates of oxygen consumption during spontaneous diving activity, it has been suggested that naturally diving animals should be capable of maintaining aerobic metabolism in all tissues for the duration of a normal dive (e.g. Eliassen, 1960). Recently, experimental evidence in favour of this suggestion has been obtained in Humboldt penguins, *Spheniscus humboldti* (Butler & Woakes, 1984), pochard, *Aythya ferina*, and tufted ducks, *A. fuligula* (Butler & Woakes, 1979; Woakes & Butler, 1983). By means of respirometry it was calculated that oxygen uptake in the voluntarily diving tufted duck increases to 3·5 times resting levels; this is similar to the levels measured when the ducks are swimming at near maximum sustainable speed on the water surface (Woakes & Butler, 1983). Heart rate was found to be elevated above resting levels throughout voluntary dives in this species.

Using measured values for the usable oxygen storage capacity of the tufted duck (Keijer & Butler, 1982) it was calculated that the ducks should be capable of remaining submerged during voluntary dives for a maximum period of 51 s (Woakes & Butler, 1983) without resorting to anaerobiosis. These data raise the question of the adaptive significance of the oxygen-conserving response (the 'classical' diving response) which is observed in all involuntarily submerged animals. Is it an artifact of the experimental situation, perhaps induced by stress (Kanwisher, Gabrielsen & Kanwisher, 1981; Smith & Tobey, 1983), or can it be evoked under certain circumstances during natural diving behaviour? Prolonged dives (i.e. dives of sufficiently long duration to require some degree of anaerobic metabolism in the active muscles) have been observed to occur occasionally in some highly adapted aquatic species: emperor penguins, *Aptenodytes forsteri* (Kooyman *et al.* 1971) and Weddell seals, *Leptonychotes weddelli* (Kooyman *et al.* 1980). It is assumed that the 'classical' diving response is invoked in these cases, although supporting evidence is available only for the Weddell seal (Kooyman & Campbell, 1972; Kooyman, Kerem, Campbell & Wright, 1973; Kooyman *et al.* 1980; Kooyman, Castellini, Davis & Maue, 1983; Hill *et al.* 1983) and no direct physiological measurements have been made in birds. It was decided, therefore, to determine whether the tufted duck will voluntarily prolong dive duration to obtain food, and to monitor heart rate during such long-duration dives. Preliminary observations (Butler, 1982, 1985) suggested that the heart rate response is very variable and tends towards a bradycardia during longer dives.

MATERIALS AND METHODS

Ten tufted ducks of either sex were used (body mass = 616·7 ± 3·6 g; mean ± S.E.). They were reared from eggs within the department's animal house. After growth of adult feathers they were transferred to an enclosed outdoor pond where they were kept until required. In addition to any natural food supply, the ducks were fed mixed grain (Heygates Ltd) which was thrown onto the water (thus encouraging the ducks to dive) and this was supplemented regularly by a supply of growers pellets (Heygates Ltd) which was provided in a covered bowl at the side of the pond.

Three weeks prior to the start of the observations the ducks were taken indoors and kept in the animal house. A purpose-built, single-channel PIM radiotransmitter was implanted into the abdominal cavity (with electrocardiogram (ECG) electrodes placed under the sternum, close to the heart) under halothane anaesthesia (1–2 % Fluothane, ICI Ltd, in a 37 % O_2/63 % N_2 mixture). Abdominal feathers were soaked in chlorhexidine (0·05 % solution) and then deflected (rather than plucked) prior to making a midline incision. Deflection of the feathers enabled the ducks to preen them over the wound on recovery from anaesthesia and this allowed the ducks to take to water without discomfort within a few hours after the operation. The ducks were given an injection of ampicillin (15 mg intramuscular Penbritin, Beechams) at the time of the implantation. Body weight and general condition were closely monitored for 2 weeks, after which the ducks with the transmitters could not be distinguished by body weight or behaviour from the others.

Two methods were used to encourage prolongation of voluntary dives: (i) dive duration was increased by training ducks to feed at various horizontal distances from the uncovered surface on an otherwise covered outdoor pond ('extended dives'), and (ii) access to the surface was, during otherwise voluntary feeding dives in an indoor tank, briefly denied them ('enclosed dives').

Extended dives

Six ducks of either sex were studied, a pair at a time, on a deep outdoor pond (10×4·5×1·9–2·8 m deep; Fig. 1). The surface of the pond was almost totally covered with plastic mesh (supported by a wooden framework) at a depth of 4 cm, except for a small uncovered area (0·9×0·9 m) in one corner. A sloping 'shallow area' (0–0·2 m deep) was also left uncovered to enable dabbling behaviour. To increase dive distance further a vertical mesh screen was erected across the width of the pond with a 0·75-m gap at one side as indicated in Fig. 1. A hinged escape hatch was fitted near to the vertical screen on the covered side to enable the ducks to resurface should they become disoriented. This hatch was left open for about 1 week, during which the ducks learned to dive around the vertical screen to all parts of the pond. When both ducks of each pair were fully familiar with the surroundings, the escape hatch was closed. Feeding stations were marked by plastic poles standing on the floor of the pond at known distances from the surface of the open section (Fig. 1). Eight such positions were simultaneously marked and food was provided at each in random order. To exclude any effects of food density on dive behaviour (Draulans, 1982), a constant quantity of grain (100 g) was spread over an approximately constant area surrounding the pole at each feed. All ducks were seen to be able to reach food at position 8 (13 m from the open surface) and the ducks were weighed every week to ensure that they were obtaining sufficient food.

Observations of behaviour were made from within a wooden hut situated 3 m from the edge of the pond. The radio signal (encoding the ECG) was received using a Sony 5090 receiver *via* a large loop antenna which was suspended over the pond. The signal was stored on one channel of a TEAC A450 stereo cassette tape recorder while the other channel was used to mark the start and end of dives and for recording a spoken commentary of the ducks' behaviour for later correlation with the decoded physiological data. The stored signal was later decoded using a purpose-built demodulator and a hard copy of the ECG was obtained using a two-channel pen

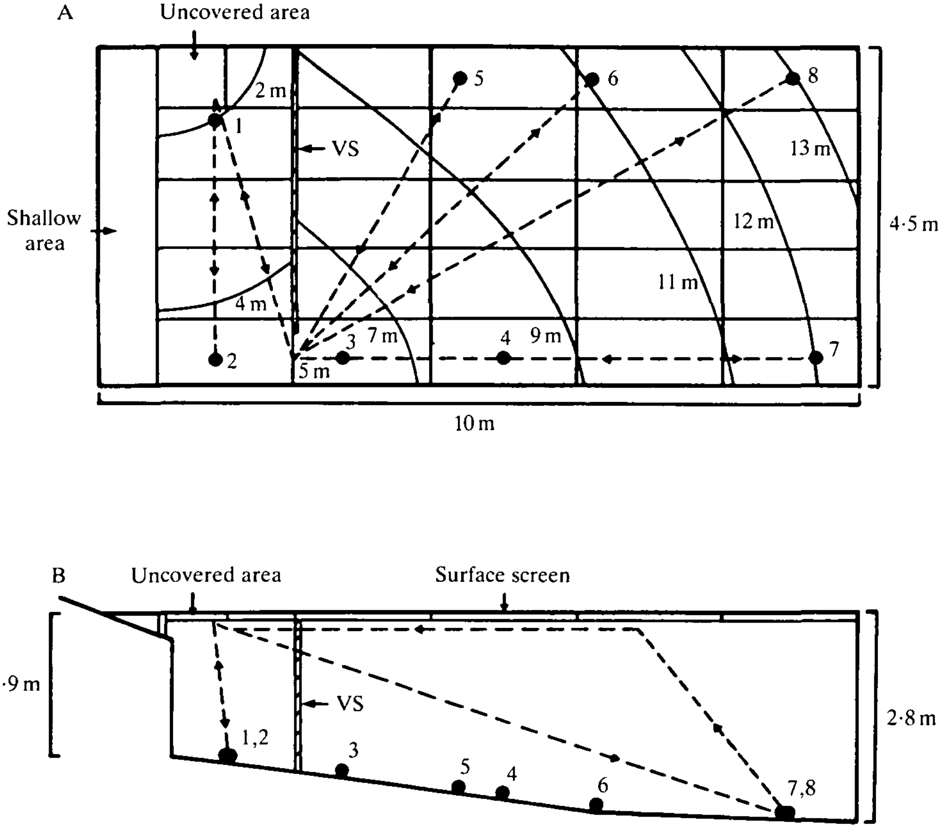

Fig. 1. Plan (A) and side elevation (B) of the outdoor pond, illustrating the positions of the feeding stations (1 to 8) in relation to the vertical screen (VS) and the uncovered section of the surface. Dashed lines represent the routes taken by the ducks to and from each feeding station. Contours represent direct distance from the water surface at the uncovered area to the floor of the pond where marked. The wooden frame supporting the surface screen divided the surface of the pond into a rectangular grid which was used to facilitate estimation of dive distance (see text).

recorder (Ormed Ltd). Heart rate was also recorded using an instantaneous rate meter (Devices Ltd).

During diving activity, dive duration (t_D), duration of inter-dive interval (t_I), number of dives per series and distance travelled to food were recorded in addition to heart rate. Confirmation of dive destination was aided by the fact that an appreciable quantity of air is lost from beneath the feathers during a dive (Butler & Woakes, 1982*a*). The division of the pond surface into a grid by the wooden framework made the precise location of the bubbles (which were normally clearly visible on the surface), and hence the horizontal location of the feeding duck, easy to estimate. Routes of ascent and descent during dives to each feeding station were observed (see Fig. 1) and total dive distance (both legs of the journey) was calculated. Horizontal, submerged swimming velocity was measured by timing the ducks swimming between two points just beneath the surface mesh on the outdoor pond. Vertical swimming velocities were measured by timing the ducks passing between two points while diving in a glass-sided indoor tank. A manually operated electronic stopwatch (Casio Electronics Co. Ltd) was used.

Time required to swim to each feeding station was calculated from the measured swimming velocities and estimated routes taken (Fig. 1). An estimate of mean time available for feeding (t_F) at each feeding station was calculated by subtraction of swimming time (t_S) from the observed mean dive durations (t_D). When dives to more than one feeding station were analysed together, mean dive distance was calculated from the proportion of dives to each station and not simply as the arithmetic mean of the distances to the feeding stations.

Heart rate was also monitored during dabbling activity, when the ducks submerged the head only to feed from the floor of the shallow area of the pond (Fig. 1), and during periods of non-diving activity and rest.

Enclosed dives

Eight ducks of either sex were used. Following transmitter implantation they were kept on an indoor glass-sided tank ($1{\cdot}63\times1\times1{\cdot}7$ m) which was divided into two sections – a larger one on which the ducks were maintained and a smaller, experimental section on which the ducks were kept individually for recording purposes. The experimental duck learned to dive from a Perspex box ($40\times40\times40$ cm) to obtain food from the floor of the tank, and heart rate was recorded (on magnetic tape as previously described) during normal feeding dives and during 'enclosed dives'. During the latter, a sliding barrier was pushed across the entrance to the box approximately 3–5 s after submersion and the duck continued to feed, apparently unaware of the barrier. The point during the dive at which the duck apparently first became aware of the barrier was noted. The barrier was reopened after a total dive duration of no longer than 30 s, which is well within the maximum dive durations recorded during the extended dives.

Mean values are given ±S.E. of the mean with the sample size (*n* or *N*) in parentheses. *N* represents the numbers of animals from which data were obtained and *n* represents the total number of observations. Mean values were obtained using

n unless sample size was low and markedly different between ducks, in which case mean values were obtained for each duck and these means were themselves used to obtain the final mean (so that sample size given $= N$). Statistical analyses were performed using a microcomputer (BBC model B) and a statistical software package (Unistat, Unisoft Ltd). Significance of differences between two means was calculated using Student's t-test assuming unequal variances. Correlation between two variables was quantified using the Pearson correlation coefficient (r). Results were considered significant at the 95 % ($P < 0{\cdot}05$) confidence level.

A preliminary report of some of the results of this study has already been presented (Butler, Stephenson & Woakes, 1986).

RESULTS

Diving behaviour

Published data have indicated that for the tufted duck, dive duration (t_D) is linearly correlated with water depth (D_w) (Dewar, 1924, 1939/40; Laughlin, 1975; Draulans & De Bont, 1980; Draulans, 1982), and combination of these data for dives of $>1{\cdot}5$ m depth gives the following equation: $t_D{}^1 = 14{\cdot}1 + 3{\cdot}43\,(\pm 0{\cdot}36) \times D_w$ (see Fig. 2). It follows from this relationship that dives longer than 50 s (i.e. the calculated mean 'aerobic dive limit' for this species) would be observed at depths of 10·5 m or more. The present study confirmed that dive duration is linearly related to distance to food (D_f). However, the increment in t_D per unit distance [$t_D = 15{\cdot}4 + 1{\cdot}61\,(\pm 0{\cdot}09) \times D_f$] was significantly smaller than that in the previous reports. The vertical mesh screen was therefore necessary to increase D_f further.

The actual distances travelled during a round trip to and from each feeding station were calculated from the routes taken (see Fig. 1) and used for calculation of swimming time (see below). During the return journeys from feeding stations 4–8, the ducks were observed to reach the surface (just beneath the surface screen) at an average of 3·0 m from the feeding station. Journeys to and from feeding stations 1–3 were direct. Due to the turbidity of the water it was not possible to make reliable observations of the routes taken during the outward journey to feeding stations 4–8. It was assumed, therefore, that the outward leg of the journey was direct to all feeding stations. It was found that rate of vertical descent was $0{\cdot}57 \pm 0{\cdot}02\,\mathrm{m\,s^{-1}}$ ($n = 155$), rate of vertical ascent was $0{\cdot}61 \pm 0{\cdot}03\,\mathrm{m\,s^{-1}}$ ($n = 143$), while submerged horizontal swimming velocity was $0{\cdot}89 \pm 0{\cdot}02\,\mathrm{m\,s^{-1}}$ ($n = 202$).

Time required to swim to each feeding station (t_S) was calculated using the calculated total distances travelled and the observed swimming velocities. Swimming time (t_S) was found to increase as a function of distance to food (D_f) at a greater rate than did t_D [$t_S = 3{\cdot}5 + 2{\cdot}21\,(\pm 0{\cdot}07) \times D_f$]. Mean time remaining for feeding (t_F) in dives to each feeding station, calculated by subtraction of t_S from mean t_D, was, therefore, negatively correlated with D_f [$r = -0{\cdot}72$; $t_F = 11{\cdot}9 - 0{\cdot}6\,(\pm 0{\cdot}1) \times D_f$], indicating that the ducks tended to reduce the amount of time spent feeding during the long-distance dives (Fig. 2).

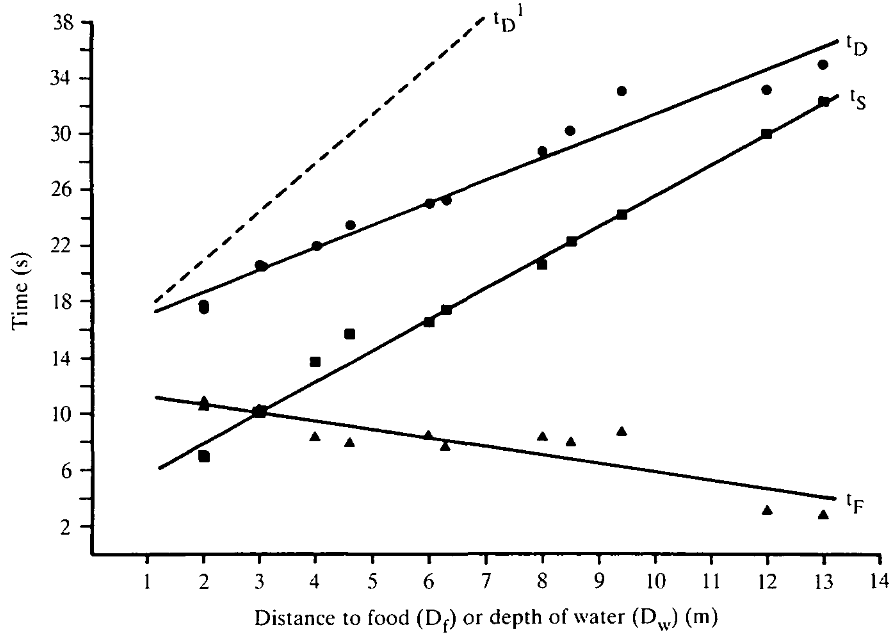

Fig. 2. Linear regression plots showing the effects of distance to food (D_f) on dive duration (t_D, circular symbols), swimming time (t_S, square symbols) and feeding time (t_F, triangular symbols in tufted ducks). The combined data of Dewar (1924, 1939/40), Laughlin (1975), Draulans & De Bont (1980) and Draulans (1982) for tufted ducks diving in water of >1·5 m depth (dashed line) relating dive duration (t_D^1) to water depth (D_w) are also illustrated. The regression equations are as follows: $t_D = 15{\cdot}4 + 1{\cdot}61\ (\pm 0{\cdot}09) \times D_f$; $t_S = 3{\cdot}5 + 2{\cdot}21\ (\pm 0{\cdot}07) \times D_f$; $t_F = 11{\cdot}9 - 0{\cdot}6\ (\pm 0{\cdot}1) \times D_f$; and $t_D^1 = 14{\cdot}1 + 3{\cdot}43\ (\pm 0{\cdot}36) \times D_w$.

The duration of inter-dive interval (t_I) was not correlated with duration or with distance of the previous or following dive; t_I was very variable and appeared to be very much dependent upon factors other than t_D or D_f, such as surface interactions between ducks or other external disturbances. The number of dives constituting a series was lower than expected; mean number (±s.e.) = 7·0 ± 0·34 ($n = 84$) and was only weakly negatively correlated with mean dive distance per series ($r = -0{\cdot}22$).

Preferred dive duration, measured by providing food uniformly over the entire pond floor both in the presence and absence of the vertical screen and/or surface screens was found to be 19·8 ± 0·19 s ($n = 472$, $N = 6$) with 83·3 % of all dives between 15 and 25 s duration. Only 7·8 % of these dives were longer than 25 s. Mean duration of dives to food at 13 m direct distance from the open surface (feeding station 8; Fig. 1) was 35·1 ± 1·34 s ($n = 100$) several dives longer than the previously reported maximum of 41 s for this species (Draulans & De Bont, 1980) were recorded; the longest was 46·3 s and was performed by a female duck. There were no detectable differences in diving ability between the sexes. Mean duration of dives to food at 2 m direct distance from the open surface (feeding station 1; Fig. 1) was 22·4 ± 0·18 s ($n = 78$, $N = 6$).

Normal feeding dives on the indoor tank were of $14{\cdot}4 \pm 0{\cdot}44$ s ($n = 50$, $N = 8$) duration. Closure of the surface gate, which occurred approximately 5 s after submersion, had no apparent effects on feeding behaviour – the ducks continued to feed on the floor of the tank and then passively returned towards the surface in the usual way. They were apparently unaware of the presence of the barrier until they had risen to within approximately 50 cm from the surface when they began actively to swim around the tank, presumably looking for a route to the surface. Swimming continued throughout the period for which the ducks were enclosed.

Heart rate during diving behaviour

The mean value of minimum resting heart rate recorded for each duck ($121{\cdot}1 \pm 14{\cdot}11$ beats min^{-1}, $n = N = 6$) is used as a reference for comparison with heart rate during the different types of diving and non-diving behaviour.

With reference to Fig. 3, dives to feeding stations 1 and 2 are referred to as 'normal dives' and dives to feeding stations 7 and 8 are referred to as 'extended dives'. Heart rate was analysed for 79 normal dives of duration $22{\cdot}4 \pm 0{\cdot}18$ s and mean water surface to food distance of $3{\cdot}8 \pm 0{\cdot}22$ m. Heart rate was also analysed for 55 long-duration, extended dives (mean ± S.E. = $41{\cdot}4 \pm 0{\cdot}32$ s) of mean water surface to food distance of $12{\cdot}6 \pm 0{\cdot}07$ m. Note that these mean distances are biased according to the number of dives to each feeding station.

Peak heart rates immediately before immersion and after emersion were slightly, but not significantly, higher for extended dives. Though not clear in Fig. 3, the onset of the pre-dive tachycardia was often abrupt and easily defined, particularly for the first dive of a series and for dives following relatively long-duration inter-dive intervals. For these dives it was found that the duration of the pre-dive tachycardia was significantly correlated with dive distance ($r = 0{\cdot}73$), ranging from $5{\cdot}1 \pm 0{\cdot}48$ s ($n = 46$) before dives to food at 2 m distance, to $10{\cdot}0 \pm 0{\cdot}73$ s ($n = 39$) for dives to food at 13 m distance. The end of the post-dive tachycardia was less easily defined, mainly as a result of the influence of non-diving activities, particularly wing flapping, preening and scratching.

Though the immediate response to submersion was unaffected by dive distance, heart rate was significantly higher in extended dives than in normal dives during the period 5–10 s after submersion while the ducks were actively swimming to the food. After 7·5 s into the dive, heart rate was steady at approximately 185 beats min^{-1} in normal dives but fell gradually (at a mean rate of $-5{\cdot}63 \pm 0{\cdot}2$ beats $\text{min}^{-1}\,\text{s}^{-1}$) in extended dives until approximately 7 s before resurfacing. Analysis of minimum heart rate recorded during the latter half of dives to all feeding stations indicates that heart rate fell to sub-resting levels (i.e. $<121{\cdot}1$ beats min^{-1}) during dives longer than approximately 35 s.

The strong correlation between dive duration and dive distance made it difficult to separate the effects of each of these on heart rate response. However, four ducks performed some exceptionally long (>25 s) normal dives of $30{\cdot}4 \pm 0{\cdot}3$ s ($n = 32$, $N = 4$) duration and $4{\cdot}9 \pm 0{\cdot}24$ m distance to food (i.e. to feeding positions 1, 2 and 3). Heart rate remained approximately stable throughout these dives, being

174·2 ± 6·5 beats min^{-1} after 22·5 s of submersion compared with a significantly lower heart rate of 139·1 ± 5·16 beats min^{-1} ($n = 65$, $N = 6$) at 22·5 s after submersion in dives of similar duration (32·1 ± 0·23 s) but greater distance to food (mean of 11·1 ± 0·26 m for the dives analysed). Thus, for dives of any given duration, heart rate adjustments were more pronounced in dives of greater distance.

The increase in heart rate to approximately resting levels in anticipation of resurfacing at the end of extended dives began approximately 7 s before breaking the surface, when the ducks were actively swimming from the food to the uncovered water surface. In contrast, at the end of normal dives, resurfacing was largely passive, the ducks ascending to the surface under the influence of their positive buoyancy. In this case there was a slight, but not significant, reduction in heart rate during the late phase of the dive (the period 3–1·5 s prior to breaking the surface) and then heart rate was seen to increase slightly at 1 s before breaking the water surface, in anticipation of resurfacing (see Fig. 3).

The heart rate responses to enclosed and normal dives on the indoor tank are illustrated in Fig. 4. Up to the point at which the ducks apparently became aware of the presence of the barrier, there were no significant differences in heart rate response between enclosed and normal dives, complementing the observations that diving behaviour was apparently unaffected up to this point. When the ducks became aware of the situation [at an average of 13·8 ± 1·02 s ($n = 31$, $N = 8$) after

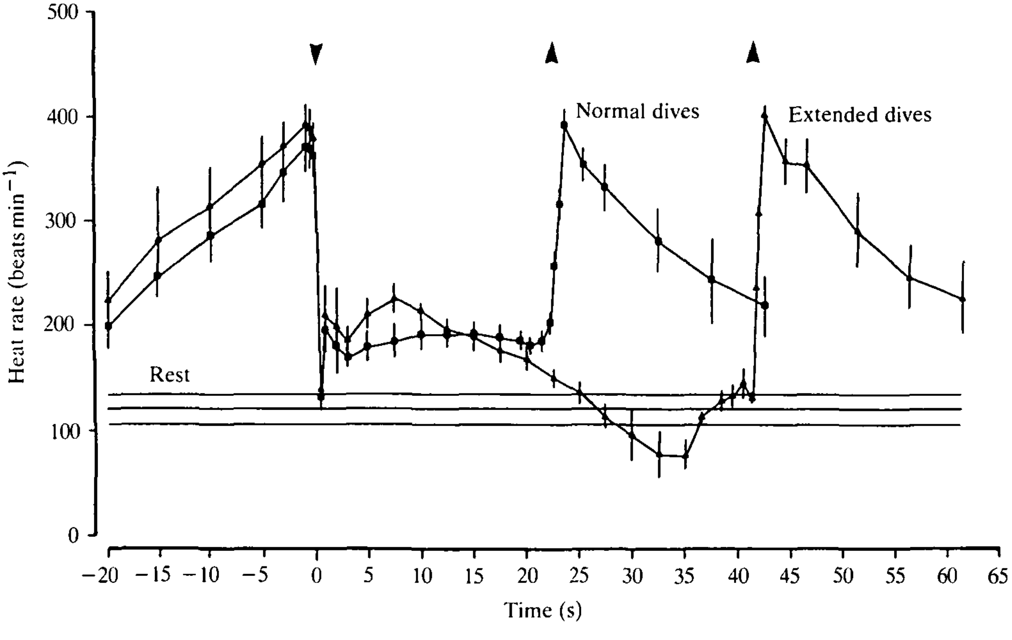

Fig. 3. Diagram of mean (±S.E.) heart rate at specific times before, during and after normal feeding dives (square symbols) and long-duration, extended dives (triangular symbols) in tufted ducks. Horizontal lines represent mean (±S.E.) of resting heart rate. Descending arrowhead (time zero) represents the point of immersion and the ascending arrowheads represent the mean points of emersion for normal feeding dives (t_D = 22·4 ± 0·18 s; $n = 79$, $N = 6$) and extended dives (t_D = 41·4 ± 0·32 s; $n = 55$, $N = 6$).

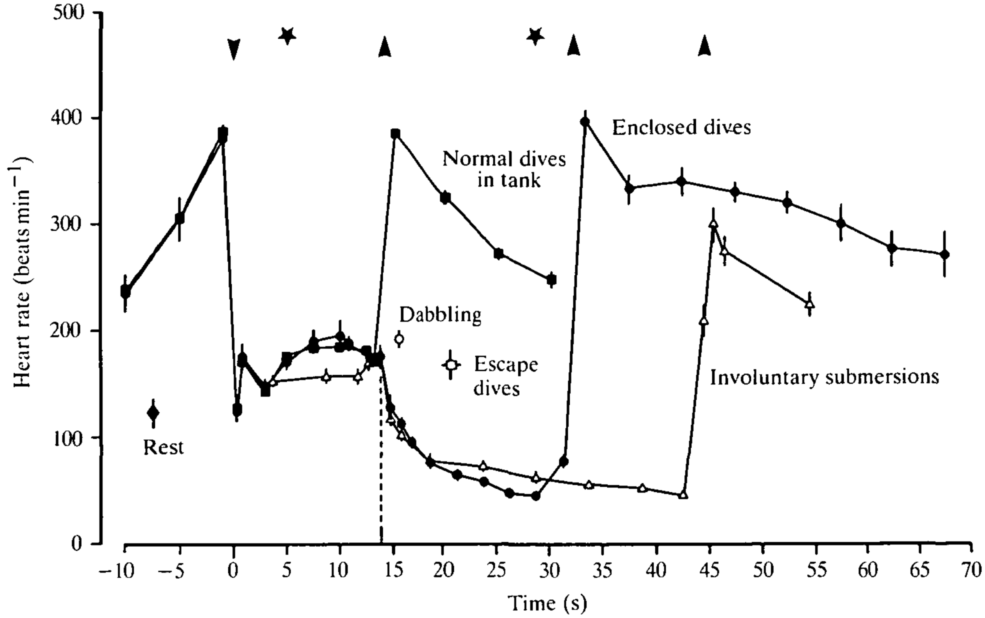

Fig. 4. Diagram of mean (±S.E.) heart rate in tufted ducks at specific times before, during and after normal feeding dives in the indoor tank (■), enclosed dives (●) and involuntary submersion (△; data from Butler & Woakes, 1982*b*). Descending arrowhead represents the point of immersion in normal feeding dives and enclosed dives (but *not* involuntary submersions). Ascending arrowheads represent the points of emersion in normal feeding dives, enclosed dives and involuntary submersion. The vertical dashed line represents the point at which the ducks apparently became aware that they were briefly unable to surface during enclosed dives (after 13·8 ± 1·02 s of submersion) and it represents the point of head immersion in the case of involuntary submersions. Asterisks represent the points of closure and opening of the sliding gate during enclosed dives. The solid diamond-shaped symbol represents mean (±S.E.) resting heart rate. The open square symbol represents mean (±S.E.) heart rate at 7·1 ± 0·9 s after immersion during 'escape dives' (Butler & Woakes, 1979) for comparison with heart rates at the same time after involuntary submersion and after the ducks became aware of the situation during enclosed dives. The open circular symbol represents mean (±S.E.) heart rate during voluntary head submersion in dabbling ducks.

submersion], there was an immediate and progressive reduction in heart rate to sub-resting levels [reaching a minimum of 46·0 ± 4·43 beats min^{-1} ($n = 25$)] which was maintained until the barrier was removed. The ducks remained active throughout this period. Upon apparently seeing the gate re-open there was often a slight anticipatory increase in heart rate prior to breaking the surface.

The heart rate data obtained by Butler & Woakes (1982*b*) during involuntary submersion of 10 tufted ducks are also illustrated for comparison. It can be seen in Fig. 4 that the bradycardia observed during enclosed dives is very similar to that observed during involuntary submersion. Minimum heart rate was the same in both situations (46·0 ± 4·43 beats min^{-1} and 45·6 ± 3·8 beats min^{-1}, respectively), though it was reached more rapidly in enclosed dives (within 15 s compared to 30 s in involuntary submersions), despite the differences in levels of physical activity.

Heart rate during recovery tachycardia was markedly increased following active enclosed dives compared with inactive involuntary submersions. At 1 s after emersion heart rates were 396·9 ± 11·25 beats min^{-1}, 385·3 ± 3·18 beats min^{-1} and 300·3 ± 15·9 beats min^{-1} following enclosed dives, normal dives in the tank, and involuntary submersions, respectively. Heart rate also remained elevated for a much longer period following enclosed dives; it was less than 250 beats min^{-1} 10 s after emersion from a 30-s involuntary submersion, and 15 s after emersion from a normal dive in the tank, but was still greater than 250 beats min^{-1} 35 s after resurfacing from enclosed dives (Fig. 4).

The heart rate response during submersion is highly labile and very much dependent upon the specific situation of each dive. Fig. 5, which illustrates mean (±S.E.) heart rate at 27 s of submersion during the different types of dive, involuntary submersion and rest, indicates that after the same time under water heart rate may be elevated above resting levels (long-duration, normal dives), it may be reduced to approximately 38 % of resting levels (enclosed dives and involuntary submersions) or it may be at intermediate sub-resting levels (extended dives).

Dabbling activity, which involves submersion of the head only, can be regarded as the type of natural behaviour which most closely resembles involuntary submersion. These voluntary head submersions were of short duration [2·7 ± 0·3 s ($n = 24$,

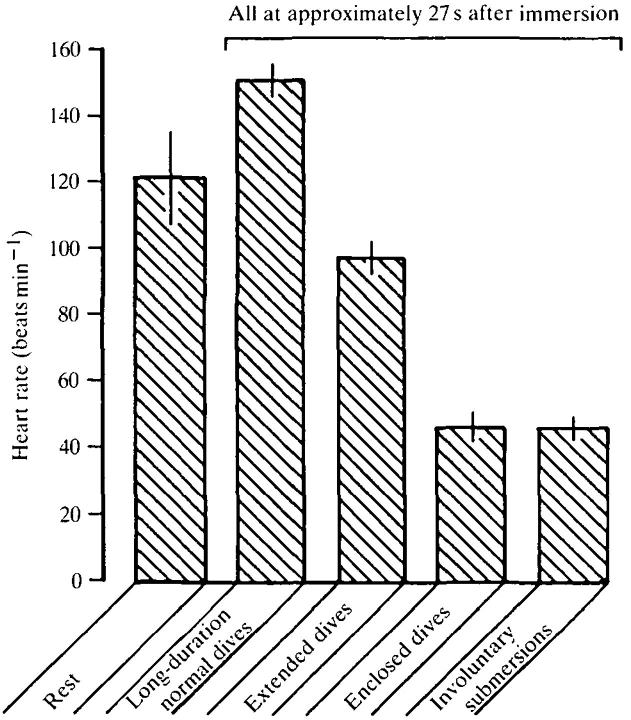

Fig. 5. Histogram illustrating mean (±S.E.) heart rate in resting tufted ducks and at approximately 27 s after immersion during three types of voluntary dives and involuntary submersion. Data for the latter from Butler & Woakes (1982*b*).

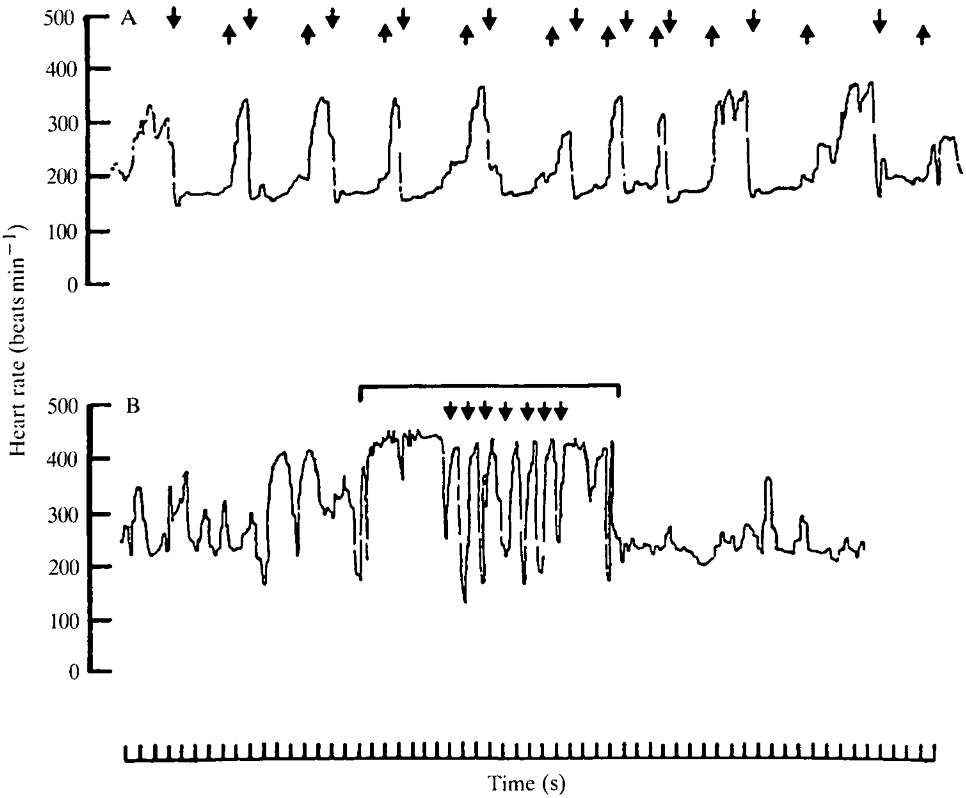

Fig. 6. Traces of instantaneous heart rate in a tufted duck recorded during (A) dabbling behaviour (where descending and ascending arrows represent points of voluntary head immersion and emersion, respectively) and (B) wing flapping combined with head submersions where the horizontal bar represents the period of continuous wing flapping and the arrows represent momentary ($0{\cdot}7 \pm 0{\cdot}03$ s duration) head submersions.

$N = 4$)] and heart rate changes were qualitatively similar to those during voluntary dives (Fig. 6A). The elevated heart rate between voluntary head submersions was $307{\cdot}5 \pm 15{\cdot}04$ beats min^{-1} (compared to $371{\cdot}8 \pm 25{\cdot}76$ beats min^{-1} prior to normal feeding dives), and this was followed by an immediate reduction in heart rate upon head immersion to $192{\cdot}3 \pm 8{\cdot}39$ beats min^{-1}. Thus, although heart rate fell upon head submersion, it always remained above the resting level. For comparison, at 2 s after immersion during normal feeding dives and involuntary submersions, mean heart rates were $181{\cdot}1 \pm 26{\cdot}1$ beats min^{-1} ($n = 79$, $N = 6$) and $104{\cdot}3 \pm 6{\cdot}2$ beats min^{-1} ($n = 36$, $N = 10$), respectively. Thus, 2 s after immersion during relatively inactive voluntary head submersions (dabbling), heart rate is significantly higher than during involuntary submersions but not significantly different from that during normal active dives (Fig. 4).

Finally, heart rate was elevated to a mean of $363{\cdot}7 \pm 7{\cdot}86$ beats min^{-1} ($n = 95$, $N = 5$) during wing flapping and when this activity was accompanied by momentary head submersions ($0{\cdot}7 \pm 0{\cdot}03$ s duration; $n = 78$, $N = 4$) heart rate fell to a mean minimum of 213·5 ± 20·7 beats min^{-1} during the periods of head submersion (Fig. 6B). Wing beating was continuous.

DISCUSSION

Diving behaviour

The finding that the dive duration *versus* distance to food relationship was significantly different in this study from all previously published data suggests that the actual depth reached during a dive may have important effects on behaviour. The important factor determining dive duration is the timing of the point at which the 'decision' to return to the surface occurs, and in the present study the ducks apparently 'decided' to return to the surface before they would have done if they had dived vertically. Possible reasons for the reduced increment in dive duration per unit distance to food in this study, compared to previous studies, are two-fold: effects due to changes in hydrostatic pressure with depth, and differences in diving energetics due to the requirement actively to swim the return leg of the journey during the present study.

Tufted ducks are bottom-feeders (Dewar, 1924) and in natural situations distance to food is determined by depth of water. Thus, increases in distance to food are normally accompanied by increases in hydrostatic pressure of 9·81 $\mathrm{kPa\,m}^{-1}$ depth resulting in increased uptake of lung oxygen stores to the blood (because of increased partial pressure of the gases in the respiratory system), and reduced buoyancy (therefore reducing the oxygen cost of locomotion) during longer dives. In the current study, where depth increased from 1·9 to 2·8 m while distance to food increased from 1·9 to 13 m (see Fig. 1), these beneficial effects of increased hydrostatic pressure were not present.

The requirement actively to swim the return leg of the journey during longer dives probably increased the oxygen cost of diving and may have contributed to the earlier timing of the 'decision' to return to the surface. However, to do this the ducks, while feeding on the bottom, must have anticipated, or learned, that extra work was required to reach the surface and adjusted behaviour accordingly. The anticipation by the ducks of increased energetic demand of long-distance dives was also suggested by the observation that duration of pre-dive preparatory tachycardia was increased as dive distance increased. Thus, if tachycardia was accompanied by hyperventilation (Butler & Woakes, 1979) there was possibly a more complete loading of oxygen and/or greater unloading of carbon dioxide prior to longer dives.

Build-up of blood carbon dioxide levels may be involved in determining the timing of the need to ventilate (and hence the 'decision' to resurface). Supporting evidence is available for hooded and harp seals, *Cystophora cristata* and *Pagophilus groenlandicus* (Påsche, 1976), the Amazonian manatee, *Trichechus inunguis* (Gallivan, 1980) and several reptiles (see Glass & Wood, 1983, for a review). Also, in humans, during non-rapid-eye-movement (NREM) sleep at high altitude, duration of sleep apnoea is related to the reduction of Pa_{CO_2} during the ventilatory phase of the cycle (Berssenbrugge, Dempsey & Skatrud, 1984). Thus, the preparatory hyperventilation and tachycardia in tufted ducks could affect diving behaviour through augmentation of oxygen stores and/or development of a hypocapnic alkalosis. It would be interesting to know the relative importance of each of these in determining the precise timing of the 'decision' to resurface during voluntary dives.

It is apparent, therefore, that the mechanisms involved in the control of the duration of the feeding time of a dive are very complex. During extended dives, where heart rate data suggest that there may be a degree of anaerobiosis, physiological factors such as changes in blood gas levels or acid–base disturbances may be involved in determining the timing of the termination of feeding. However, during normal feeding dives, where distance to food was markedly shorter, the duration of feeding time was not notably greater (see Fig. 2). During normal feeding dives, therefore, duration of feeding time is probably not under the influence of the above-mentioned physiological factors since the ducks probably remain fully aerobic throughout these relatively short-duration dives (Woakes & Butler, 1983), and in this case feeding time may be influenced by a number of other factors such as food density, particle selection time and handling time (Draulans, 1982) and/or by the rate of food ingestion.

Extrapolation of the regression line for feeding time (t_F) in Fig. 2 to the abscissa indicates that, under the conditions of the present study, at a distance of 19·8 m to food no time would be available for feeding, and mean dive duration would be 47·3 s. This theoretical maximum dive duration, calculated from behavioural observations, is very close to the observed maximum dive duration of 46·3 s and is only slightly less than the theoretical maximum dive duration of 51 s calculated from physiological data (Woakes & Butler, 1983). The observation that t_F decreases and number of dives per series remains the same (or falls slightly) as a function of distance to food indicates that to maintain energy balance the ducks must have either increased the rate of energy (food) intake per dive and/or increased the number of series of dives per day. These possibilities were not tested.

Contrary to previous observations (Dewar, 1924; Draulans & De Bont, 1980), the highly variable duration of inter-dive interval observed in the ducks in the present study suggests that optimization of the proportion of time spent under water was not of primary importance. This could have resulted from the fact that in this study the ducks were in pairs, whereas in other studies they were usually in a flock. The increased requirement for vigilance as an anti-predator strategy in this study may have taken precedence over the advantages incurred by optimization of foraging (diving) behaviour.

Heart rate

The immediate conclusion that can be drawn from the results of this study is that the heart rate response to submersion, at least in this species, is very variable and very much dependent upon the precise conditions under which the submersion takes place. Two factors appear to be particularly important: the level of physical activity and the psychological state of the animal.

In confirmation of previous work (Butler & Woakes, 1979, 1982*b*; Woakes & Butler, 1983) heart rate was elevated above resting levels throughout normal feeding dives. This compares with the decline to very low sub-resting levels in ducks involuntarily submerged in water (Butler & Woakes, 1982*b*). The present study has shown that the ducks could switch between these two extreme responses during a dive, either gradually (during extended dives) or more rapidly (during enclosed dives). If sub-resting heart rates during submersion are representative of the occurrence of the oxygen-conserving response ('classical diving response') then these results indicate that, like the Weddell seal (Hill *et al.* 1983), the tufted duck is capable of invoking this response when there is a need to remain under water for unusually long times. The role of fear or stress in mediating the development of the 'classical' response to involuntary submersion is a matter of debate (Kanwisher *et al.* 1981; Butler & Jones, 1982; Blix & Folkow, 1983; Smith & Tobey, 1983; Gabrielsen, 1985). The full bradycardia in freely diving tufted ducks was seen, during enclosed dives, only when the animals were aware of the situation, suggesting a powerful influence of the suprabulbar nervous structures in cardiovascular control. However, it was shown by Butler & Woakes (1979) that heart rate during escape dives of tufted ducks is similar to that seen during spontaneous feeding dives; it is now clear that it is also significantly above that during enclosed dives and involuntary submersions (see Fig. 4). The main difference between these situations is that during enclosed and involuntary submersions the ducks could not predict the duration for which lung ventilation was inhibited, whereas during feeding dives and escape dives access to air was not impeded.

It is interesting to speculate as to the mechanisms involved in the development of bradycardia during extended and enclosed dives. The cardioinhibitory effect of carotid body chemoreceptor stimulation is of increasing importance during the course of voluntary dives in tufted ducks (Butler & Woakes, 1982*b*) and current work suggests that carotid body chemoreceptor stimulation forms part, but not all, of the mechanism resulting in bradycardia during extended and enclosed dives (R. Stephenson & P. J. Butler, in preparation).

Stimulation of nasal receptors is primarily responsible for the onset of bradycardia during involuntary submersion of the redhead duck, *Aythya americana*, though it is only partly involved in the initiation of the cardiac response to voluntary dives (Furilla & Jones, 1986). If the situation is the same in the closely related tufted duck, then it would be reasonable to speculate that nasal receptor stimulation may be involved in the onset of bradycardia during enclosed dives. The cardiac responses to involuntary submersion and enclosed dives in tufted ducks were very similar, despite the fact that the onset of the bradycardia occurred at the time of head submersion in the case of involuntary submersions, but was initiated some 14 s after submersion in the case of enclosed dives. This suggests that during normal dives the nasal reflexes are inhibited, possibly by a central nervous mechanism, or by habituation, and sudden activation of the oxygen-conserving response during enclosed dives is brought about by their disinhibition.

Studies in freely diving birds and mammals have emphasized the opposing requirements imposed by the asphyxia of submersion and by exercise (e.g. Millard, Johansen & Milsom, 1973; Butler, 1982; Hochachka & Somero, 1984; Castellini, 1985) and it has been suggested that the cardiovascular adjustments during normal voluntary dives of tufted ducks result from a balance between the 'classical' response to involuntary submersion and the responses to exercise, with the bias towards the latter (Butler, 1982).

In surface-swimming tufted ducks heart rate was found to be linearly related to power input (Woakes & Butler, 1983) and in the present study heart rate was correlated with activity levels during non-diving behaviour (i.e. in normally ventilating ducks). However, the role of any reflex effects of muscle activity on the cardiovascular system during diving activity was not clear. If afferent information from the active muscles is involved in maintaining the exercise component of the response to normal dives, the response to enclosed dives shows that this can be completely inhibited under certain circumstances. The rates of reduction in heart rate are very similar during enclosed dives and involuntary submersions, despite the fact that in the former the ducks were swimming throughout the period of submersion while in the latter they were inactive. Furthermore, during dabbling behaviour, when the ducks voluntarily submerged the head to feed but were otherwise relatively inactive, heart rate was similar to that during normal active dives and significantly above that during inactive, involuntary head submersions (Fig. 4). Wing flapping activity, which involved exercise of the relatively large pectoral muscle mass, was accompanied by an elevation of heart rate to over 350 beats min^{-1}. However, heart rates in excess of this were observed in relatively inactive ducks during preparation just prior to diving. In both of these cases, an immediate reduction in heart rate accompanied head immersion, even when muscular activity continued (Fig. 6). Thus, any reflex effect of muscle afferent information on heart rate is highly susceptible to modulation.

The work of Woakes & Butler (1983) and the results of the present study highlight the need for a physiologically more meaningful, and more precise, definition of the term 'bradycardia'. The term has usually been used to describe a reduction in heart rate to below either the resting value or the pre-dive value. The reduction in heart rate below the resting level during involuntary submersion, enclosed dives and in the latter part of extended dives is classed as a bradycardia by either definition and it illustrates that a 'classical' diving bradycardia will occur in active ducks behaving normally. Heart rate during normal dives in the tufted duck, however, would be interpreted as bradycardia using the 'pre-dive heart rate' definition (though it is probably more realistic to view the reduction in heart rate upon immersion as a cessation of a pre-dive tachycardia rather than the onset of a bradycardia) but not when using the 'resting heart rate' definition. Woakes & Butler (1983) measured oxygen uptake and heart rate in tufted ducks during diving and during surface swimming at various speeds. There was a linear relationship between heart rate and oxygen uptake during surface swimming, and further analysis of their results shows that the relationship between overall mean oxygen uptake and mean heart rate during total diving activity (i.e. over entire series of dives) is not significantly different from that during surface swimming (Stephenson, 1985). They found, however, that at the same level of oxygen uptake, heart rate during normal dives is significantly lower than that recorded when the ducks were swimming on the surface.

It would seem sensible, therefore, to define 'bradycardia' as a reduction in heart rate below the value which is 'normal' for a given level of activity. Surface swimming probably represents the closest approximation to diving exercise in normally ventilating ducks, and if the heart rate *versus* oxygen uptake relationship during surface swimming can be considered 'normal' for this type of activity in ducks then, by this definition, the heart rate during voluntary dives represents a bradycardia (Woakes & Butler, 1983). Provided there is no increase in cardiac stroke volume, the occurrence of a 'bradycardia' during voluntary dives implies a reduction in cardiac output. Since total oxygen uptake was the same as during surface swimming, arterio-venous O_2 content difference must have increased during diving compared with surface swimming. It is likely that vasoconstriction in non-active tissues (including respiratory muscles) was enhanced during diving to effect a degree of oxygen conservation in these tissues, while oxygen consumption by the active leg muscles was actually higher during diving than during surface swimming at the same level of total oxygen uptake (Butler, 1982).

To conclude, tufted ducks utilize both behavioural and physiological mechanisms to counteract constraints imposed during diving activity under various conditions. During extended diving activity, which must be relevant to the situation encountered by ducks feeding under ice in winter, an oxygen-conserving response (as indicated by heart rate) is gradually invoked. To prevent a pronounced metabolic acidosis it is likely that the active leg muscles are perfused and remain aerobic for as long as possible, the majority of oxygen conservation taking place in non-active tissues (and this may lead to a slight accumulation of lactic acid in these tissues). Under situations when access to air is temporarily impaired, as may occur if the animal becomes disoriented under ice, a full oxygen-conserving response occurs, even though the ducks may remain active, and the implication is that even the leg muscles experience vasoconstriction, reduced perfusion and (after depletion of myoglobin-bound oxygen stores) anaerobiosis.

This work was supported by the Science and Engineering Research Council.

REFERENCES

BERSSENBRUGGE, A., DEMPSEY, J. & SKATRUD, J. (1984). Hypoxic versus hypocapnic effects on periodic breathing during sleep. In *High Altitude and Man* (ed. J. B. West & S. Lahiri), pp. 115–127. Baltimore: Waverly Press Inc.

BLIX, A. S., ELSNER, R. & KJEKSHUS, J. K. (1983). Cardiac output and its distribution through capillaries and A–V shunts in diving seals. *Acta physiol. scand.* **118**, 109–116.

BLIX, A. S. & FOLKOW, B. (1983). Cardiovascular adjustments to diving in mammals and birds. In *Handbook of Physiology*, vol. 3, *The Cardiovascular System* (ed. J. T. Shepherd & F. M. Abboud), pp. 917–945. Bethesda: American Physiological Society.

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

BUTLER, P. J. (1985). The diving reflex in free-diving birds. In *Arctic Underwater Operations* (ed. L. Rey), pp. 49–61. London: Graham & Trotman.

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

BUTLER, P. J., STEPHENSON, R. & WOAKES, A. J. (1986). Variability of the heart rate response during voluntary diving in the tufted duck, *Aythya fuligula*. *J. Physiol. Lond.* **371**, 69P.

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. (1982*a*). Telemetry of physiological variables from diving and flying birds. *Symp. zool. Soc. Lond.* **49**, 106–128.

BUTLER, P. J. & WOAKES, A. J. (1982*b*). 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. (1984). Heart rate and aerobic metabolism in Humboldt penguins, *Spheniscus humboldti*, during voluntary dives. *J. exp. Biol.* **108**, 419–428.

CASTELLINI, M. A. (1985). Closed systems: resolving potentially conflicting demands of diving and exercise in marine mammals. In *Circulation, Respiration and Metabolism* (ed. R. Gilles), pp. 219–226. Berlin: Springer-Verlag.

DEWAR, J. M. (1924). *The Bird as a Diver*. London: H. F. & G. Witherby.

DEWAR, J. M. (1939/40). Timing the underwater activities of diving birds. *British Birds* **33**, 58–61.

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

DRAULANS, D. & DE BONT, A. F. (1980). Een analyse van het duiken naar voedsel van de kuifeend, *Aythya fuligula*, buiten het broedseizoen. *Le Gerfaut* **70**, 251–260.

ELIASSEN, E. (1960). Cardiovascular responses to submersion asphyxia in avian divers. *Arbok. Univ. Bergen Mat. Naturv. Ser.* **2**, 1–100.

FURILLA, R. A. & JONES, D. R. (1986). The contribution of nasal receptors to the cardiac response to diving in restrained and unrestrained redhead ducks (*Aythya americana*). *J. exp. Biol.* **121**, 227–238.

GABRIELSEN, G. W. (1985). Free and forced diving in ducks: habituation of the initial dive response. *Acta physiol. scand.* **123**, 67–72.

GALLIVAN, G. J. (1980). Hypoxia and hypercapnia in the respiratory control of the Amazonian manatee (*Trichechus inunguis*). *Physiol. Zool.* **53**, 254–261.

GLASS, M. L. & WOOD, S. C. (1983). Gas exchange and control of breathing in reptiles. *Physiol. Rev.* **63**, 232–260.

HILL, R. D., SCHNEIDER, R. C., LIGGINS, G. C., HOCHACHKA, P. W., SCHUETTE, A. H. & ZAPOL, W. M. (1983). Microprocessor controlled recording of bradycardia during free diving of the antarctic Weddell seal. *Fedn Proc. Fedn Am. Socs exp. Biol. (Abstr.)* **42**, no. 1045, p. 470.

HOCHACHKA, P. W. & SOMERO, G. N. (1984). *Biochemical Adaptation*. Princeton: Princeton University Press.

IRVING, L. (1934). On the ability of warm-blooded animals to survive without breathing. *Sci. Mon.* **38**, 422–428.

IRVING, L. (1939). Respiration in diving mammals. *Physiol. Rev.* **19**, 112–134.

JONES, D. R., BRYAN, R. M., WEST, N. H., LORD, R. H. & CLARK, B. (1979). Regional distribution of blood flow during diving in the duck (*Anas platyrhynchos*). *Can. J. Zool.* **517**, 995–1002.

KANWISHER, J. W., GABRIELSEN, G. & KANWISHER, N. (1981). Free and forced diving in birds. *Science* **211**, 717–719.

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. & CAMPBELL, W. B. (1972). Heart rates in freely diving Weddell seals, *Leptonychotes weddelli*. *Comp. Biochem. Physiol.* **43**A, 31–36.

KOOYMAN, G. L., CASTELLINI, M. A., DAVIS, R. W. & MAUE, R. A. (1983). Aerobic diving limits of immature Weddell seals. *J. comp. Physiol.* **151**B, 171–174.

KOOYMAN, G. L., DRABEK, C. M., ELSNER, R. & CAMPBELL, W. B. (1971). Diving behaviour of the emperor penguin, *Aptenodytes forsteri*. *Auk* **88**, 775–795.

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., 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.* **138**B, 335–346.

LAUGHLIN, K. F. (1975). The bioenergetics of the tufted duck (*Aythya fuligula*). Ph.D. thesis, University of Stirling.

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

PÅSCHE, A. (1976). The effect of hypercapnia on respiratory characteristics and diving behaviour of freely diving seals. *Respir. Physiol.* **26**, 183–194.

SCHOLANDER, P. F. (1940). Experimental investigations on the respiratory function in diving mammals and birds. *Hvalradets Skr.* **22**, 1–131.

SMITH, E. N. & TOBEY, E. W. (1983). Heart-rate response to forced and voluntary diving in swamp rabbits *Sylvilagus aquaticus*. *Physiol. Zool.* **56**, 632–638.

STEPHENSON, R. (1985). The physiology of natural diving behaviour in the tufted duck (*Aythya fuligula*). M.Sc. (Qual.) thesis, University of Birmingham.

WOAKES, A. J. & BUTLER, P. J. (1983). Swimming and diving in tufted ducks, *Aythya fuligula*, with particular reference to heart rate and gas exchange. *J. exp. Biol.* **107**, 311–329.