

CARDIAC OUTPUT AND BLOOD FLOW DISTRIBUTION DURING SWIMMING AND VOLUNTARY DIVING OF THE TUFTED DUCK (*AYTHYA FULIGULA*)

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Summary

Cardiac output (\dot{V}_b) and blood flow distribution were continuously measured in the tufted duck when diving voluntarily. Blood flows through pulmonary, ischiadic, carotid and brachiocephalic arteries were recorded using miniature pulsed Doppler flow probes. By measuring these flows, cardiac output and blood flow to the leg muscles and to the flight muscles could be calculated.

Heart rate and \dot{V}_b were well correlated, making the former a very good indicator of any changes in the latter. Blood flow to the leg muscles increased substantially during both swimming and diving to five times the resting rate. Cardiac output, though, was lower during the later portions of a dive than it was during swimming. A consequence of this lower \dot{V}_b was that the proportion of \dot{V}_b supplying the leg muscles was much greater during diving than it was whilst the duck was swimming. This indicates that more extensive peripheral vasoconstriction was occurring during diving. The blood flow to the wing muscles during diving was found to be significantly lower than that at rest but there was no net change in blood flow through the brachiocephalic arteries as the blood flow to the head increased.

Peripheral vasoconstriction must, therefore, have been occurring in other parts of the body during diving, possibly within the vascular beds supplying the gastrointestinal tract, the skin and the respiratory muscles. This study supports the prediction that voluntary diving in tufted ducks is a compromise between the physiological response to involuntary submergence and that to exercise in air, but with the bias towards the latter.

Introduction

Experiments to determine the physiological responses to diving in animals have, in the main, concentrated on involuntary submergence (e.g. Scholander, 1940; Folkow *et al.* 1967; Johansen, 1964; Jones *et al.* 1979). From these and other studies, an orchestrated set of physiological adjustments has been recorded that constitutes what has been termed the 'classical' dive response. The cardiovascular

Key words: diving, swimming, tufted duck, *Aythya fuligula*, cardiac output, blood flow.

adjustments associated with this response include a selective peripheral vasoconstriction (causing an overall increase in peripheral resistance) in those tissues that can obtain their energy requirements through anaerobic metabolism. At the same time there is a decrease in cardiac output, so maintaining blood pressure at pre-dive levels. These adjustments conserve the limited oxygen stores for those tissues that are oxygen-dependent, e.g. central nervous tissue and myocardium.

However, there are a number of important differences between involuntary and voluntary diving that make any comparison between the two difficult. First, when diving voluntarily, most animals are also active (diving being primarily a foraging activity), which is not normally the case during involuntary dives. This will result in a greater energy demand by the active locomotor muscles, and any anaerobic metabolism would be accompanied by a build up of lactic acid, which would eventually cause the muscle to fatigue (Folkow *et al.* 1966; Fitts and Holloszy, 1976; Stamford *et al.* 1981; Yates *et al.* 1983; Furilla and Jones, 1987a). A second drawback in making comparisons between voluntary and involuntary dives is that the former are, in general, much shorter than the latter. For example the tufted duck can tolerate involuntary submersion for several minutes, but its normal dive duration is between 10 and 20 s (Butler and Woakes, 1979, 1982; Draulans, 1982). Coupled with this is the fact that most animals probably have sufficient oxygen stores held within the body (in the blood, lungs and tissues) to enable them to maintain aerobic metabolism in all tissues during these normal dives even when the metabolic rate is considerably elevated (Eliassen, 1960; Kooyman *et al.* 1971; Woakes and Butler, 1983).

Animals performing sustained exercise with free access to air show increases in cardiac output and in the blood flow to the working muscles. This response is invoked, primarily, to transport the extra oxygen required by the working muscle and to remove waste products. Blood flow may also be redistributed away from the inactive muscles and viscera (Fixler *et al.* 1976; Butler *et al.* 1988). As birds have two independent sets of locomotory muscles, the flight muscles and those associated with the legs, used for running, diving etc., there is greater scope for blood flow to be redistributed from the inactive to the active muscles during exercise than is the case in a quadrupedal mammal, where nearly all the muscles are used during locomotion (Musch *et al.* 1987).

It can therefore be seen that this 'exercise' response (peripheral vasodilation and tachycardia) is in conflict with the 'classic' dive response (peripheral vasoconstriction and bradycardia). It has been proposed that, in the tufted duck at least, the physiological adjustments to voluntary diving will be a modification of the exercise response (Butler, 1982). This proposal is based on the observation that oxygen consumption during voluntary diving is similar to that whilst the ducks are swimming at maximum sustainable speed. Heart rate, however, is lower during diving (although it is much higher than during involuntary submergence), and this is taken to indicate that cardiac output is lower and that some peripheral vasoconstriction is occurring (Butler, 1982). This hypothesis has gained some support from qualitative studies using ^{99m}Tc -labelled macro-aggregated albumin

(Jones *et al.* 1988) showing that the blood flow to the legs, heart and brain are elevated during voluntary diving but that the blood flow to the pectoral muscles is reduced. This is a similar pattern of blood flow distribution to that seen in the swimming duck (Butler *et al.* 1988).

The purpose of this study was to monitor the changes in cardiac output and blood flow through various arteries during voluntary diving in the tufted duck (*Aythya fuligula* L.) and during swimming when the birds have free access to air.

Materials and methods

Tufted ducks of either sex were trained to dive in shallow indoor tanks (see Bevan *et al.* 1992). When an animal would dive for a mean dive duration of between 10 and 15 s, miniature pulsed Doppler flow probes (TMI Ltd) were implanted around various arteries to measure the blood flows.

Birds were assigned to one of two groups. Group I birds had flow probes implanted around the right pulmonary and ischiadic arteries. By doubling the pulmonary flow, the cardiac output (\dot{V}_b) can be estimated. The ischiadic artery supplies the active leg muscles (West *et al.* 1981). Group II birds had flow probes implanted around the left brachiocephalic and left carotid arteries. The brachiocephalic artery supplies the head and the wing muscles, and the carotid artery supplies the head. By subtracting the two flows from each other the blood flow along the brachial artery, primarily supplying the wing muscles, can be estimated. Six birds were assigned to group I and five to group II. In this study it was assumed that the flow along the left and right arteries is similar and that the probe does not affect the flow along that artery (see Grant *et al.* 1988). Hence, all measured flows were doubled and are reported as such unless otherwise stated.

The miniature pulsed Doppler flow probes (TMI Ltd) were prepared for implantation by encasing the wires leading from the probe in silastic tubing. The free ends of the wires were soldered onto small metal plugs (RS Components Ltd), which were individually encased in heat-shrink tubing (RS Components Ltd) and filled with Araldite to make a small connector.

Surgical procedures

The birds were anaesthetised with an intramuscular injection of either equithesin (for composition see Fedde, 1978) or a combination of ketamine hydrochloride (Vetlar) and metomidate (Hypnodil). They were artificially ventilated at 20 breaths min^{-1} with a tidal volume of 20 ml. Body temperature was kept constant throughout surgery with a heated blanket controlled by a thermocouple inserted approximately 2 cm into the cloaca.

The feathers in the intraclavicular region were soaked in chlorhexidine and deflected to expose the skin. A midline incision was made through the skin and the cranial air sac, exposing the inside of the thoracic cavity. The right pulmonary, the left brachiocephalic and the left carotid arteries were identified. The connective tissue surrounding the appropriate vessel was teased away, care being taken to

avoid damaging any nerves, and a miniature pulsed Doppler flow probe (TMI Ltd) was placed around the artery and held in place with suture thread (Davis and Geck). Ultrasound gel was injected between the probe and the artery to ensure a good acoustical contact between the crystal and the arterial wall. The signal from the probe was checked by attaching it to a directional pulsed Doppler flowmeter (model no. 545C-4, Bioengineering, University of Iowa). The leads were led out of the thoracic cavity and the air sac was closed with chromic catgut (Ethicon Ltd). The leads were passed subcutaneously to the neck (where it was difficult for the bird to reach them with its beak) and led to the exterior. The incision in the skin was sewn together with suture thread (Davis and Geck) and the area covered with wound dressing powder (Veterinary Drug Co. Ltd). In group I birds, an incision was also made in the skin covering the right thigh and, using blunt dissection, the muscle blocks were parted to reveal the ischiadic artery. A flow probe was placed around the artery and the wound closed as indicated above.

The leads from the different flow probes were colour-coded to differentiate between them. After the operation, the birds were given an injection of Penbritin (0.025 ml, 15 mg 100 ml⁻¹; Ampicillin, Beechams Ltd) and allowed to recover whilst still being warmed by the heated blanket. When the bird had fully recovered from the anaesthetic, it was placed back in its tank. An injection of Penbritin was given daily for the next week to counter any possible infection. Within a week the ducks were diving voluntarily and the training programme was resumed. Approximately 1 month after the operation it was possible to record from the implanted flow probes.

Experimental protocol

When the birds had fully recovered and were diving normally, the flow probes were connected to a flow meter (545C-4, Bioengineering) *via* a purpose-built lead long enough for the duck to reach the bottom of the tank. In order that the lead should remain free from the duck during diving, it was passed over a pulley that could be raised and lowered by the experimenter. The outputs of the flow probes were adjusted for the best signal, and both mean and pulsatile flows were displayed on an eight-channel chart recorder (Lectromed Ltd). Heart rate, obtained by passing the differentiated pulmonary flow signal through an instantaneous rate meter (Devices Ltd), was also displayed. The pulsatile flow signals were also recorded on a four-channel tape recorder (Racal Store 4D). The birds were allowed to recover from the handling for at least one 1 h before the training programme was started, after which the programme was set to elicit dives of between 10 and 20 s duration. During an experiment, the times when a dive started and finished and the temperature of the water were marked on the pen recorder paper.

The birds were also trained to swim on a variable-speed water channel (Armfield Engineering Ltd). For a full description of the water channel see Woakes and Butler (1983). The water velocity could be varied between 0 and 1.3 m s⁻¹ as measured with a Braystoke current flowmeter (model BFMOO2,

Valeport Developments Ltd). The birds were restricted to a section of the water channel 1.0 m long by 0.5 m wide, with a water depth of 0.4 m, and were trained to swim at various speeds until they could swim at their maximum sustainable swimming speed (U_{\max} ; approximately 0.8 ms^{-1} , Woakes and Butler, 1983). Training took place both prior to any surgical procedures and during the post-recovery period.

After training had been completed, the blood flows and heart rate were recorded at different water speeds. The mean and pulsatile blood flows and heart rate were all displayed on an eight-channel pen recorder (Lectromed Ltd).

The blood flow traces were transferred to a computer (BBC model B) using a GTCO Digipad 5 (S.S.I. Ltd). A computer program extracted the mean blood flow (in volts) during every cardiac cycle occurring in the analysis period. These values were quantified after the flow probes had been calibrated. For comparing the variables measured during resting, swimming and diving, swimming values were taken when the birds had achieved steady-state conditions, whilst diving values were taken over the last 5 s of a dive, excluding the data in the final second when anticipatory changes prior to surfacing may occur.

Flow probe calibration

At the end of a series of experiments, the birds were killed by an overdose of pentobarbitone (Euthatal), and the arteries around which the flow probes were attached were excised with the probes *in situ*. Owing to the length of time that the flow probes had been implanted, they were always held in position by fibrolytic growth. Consequently, the position of the probe relative to the vessel did not change during calibration. The probes were calibrated by passing blood through the arteries with a pulsatile pump (Metcalf and Butler, 1982) and timing the collection of blood from the drainage tube. In the case of the ischiadic artery, it was possible to calibrate the probe *in situ* by cannulating the artery both upstream and downstream of the flow probe and passing blood from the pulsatile pump through the vessel. For all the flow probes, the coefficients of linear correlation between the flows and the voltage output from the flowmeter were of the order of 0.98.

Mean values are given \pm s.e.m. A significant difference between means was tested with Student's *t*-test or the paired *t*-test, as appropriate, using the MINITAB statistical package. Significance was tested at the 95 % confidence level.

Results

Diving

Group I birds

Data were recorded from 103 dives performed by six ducks. The mean dive duration was $15.4 \pm 1.4 \text{ s}$ (mean \pm s.e.m.). A tracing of the mean and phasic pulmonary and ischiadic blood flows is shown in Fig. 1. The peak pulmonary blood flow remained fairly constant throughout the dive, regardless of changes in heart

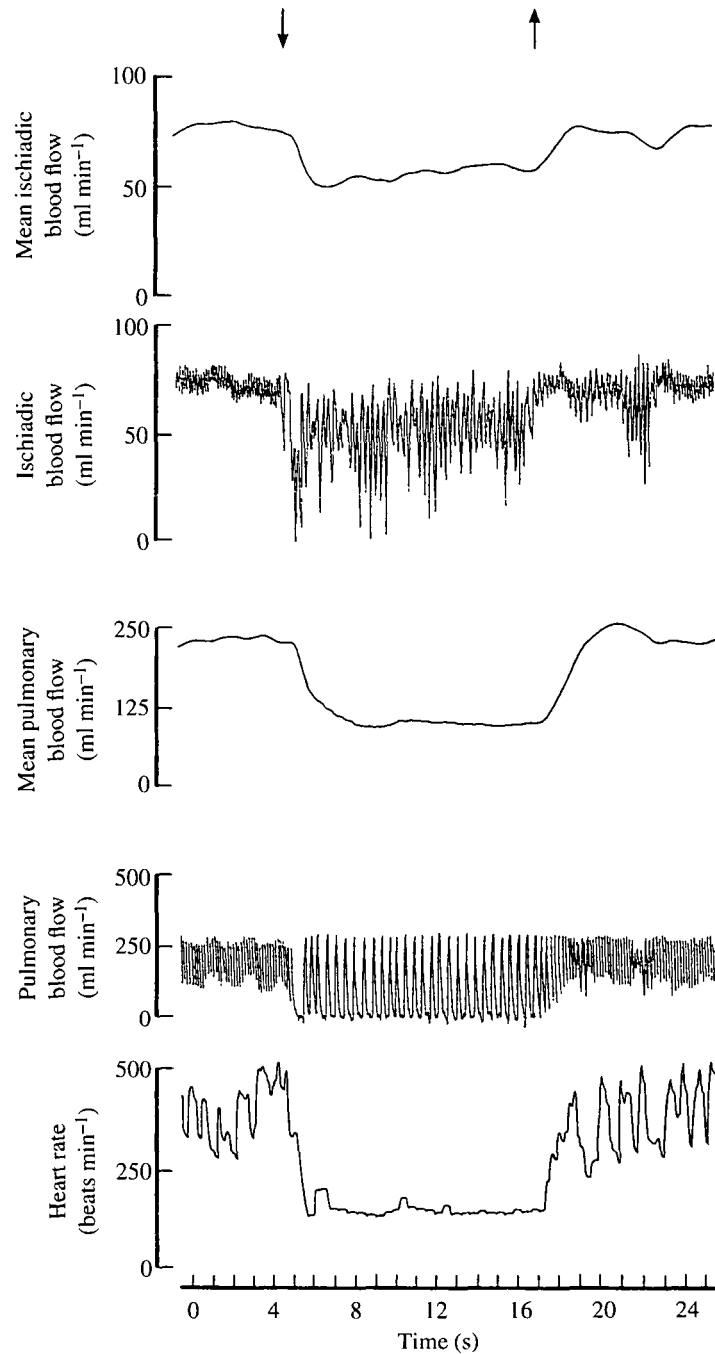


Fig. 1. Representative example of a tracing of the mean and pulsatile ischiadic and pulmonary arterial blood flows and of heart rate from a dive performed by a male tufted duck. The points at which the animal submerged and surfaced are represented by downward and upward arrows, respectively.

rate. When the bird dived, however, there was a marked fall in the pulmonary diastolic flow. The interference superimposed on the ischiadic blood flow during diving, which was not apparent on the trace of blood flow through the pulmonary artery, was probably the result of the working muscles contracting and relaxing around the vascular bed supplied by the artery.

Fig. 2 illustrates the mean changes in heart rate (f_H), cardiac output (\dot{V}_b) and cardiac stroke volume (V_s) that occurred during diving. f_H followed the normal pattern for a voluntary dive. \dot{V}_b followed the changes in heart rate, with peak values recorded during the pre-dive and post-dive tachycardias (698.8 ± 33.2 and 780.4 ± 35.0 ml min⁻¹ kg⁻¹, respectively). \dot{V}_b is the product of f_H and V_s , and the latter also varied during a dive. During the pre-dive tachycardia, V_s was at sub-resting levels, but on submersion it rose to a peak of 3.62 ± 0.32 ml kg⁻¹, 42% greater than at rest. It then fell gradually during a dive, until it again reached sub-resting levels during the post-dive tachycardia.

The blood flow through both ischiadic arteries (\dot{V}_i) during diving was always elevated above that at rest (Fig. 3A). During the pre-dive tachycardia, \dot{V}_i was 159 ± 4 ml min⁻¹, more than five times the resting rate. It declined on diving to 63 ± 9.4 ml min⁻¹, but increased throughout the rest of the dive. The highest flows recorded through the ischiadic artery were found at the end of a dive. As \dot{V}_b remained fairly stable during a dive whilst \dot{V}_i increased steadily, the proportion of \dot{V}_b supplying the ischiadic arteries increased during the dive (Fig. 3B).

The mean \dot{V}_b and f_H during diving were significantly greater than those at rest. Over the same period, the mean V_s was slightly, but not significantly, above the resting level. The greatest change seen was in \dot{V}_i which, over the later stages of a dive, was 5.1 times the resting level. The proportion of \dot{V}_b supplying the ischiadic arteries rose from $14.2 \pm 1.6\%$ at rest to $57.2 \pm 2.2\%$ during the dives (Table 1).

Both \dot{V}_b and V_s were highly dependent on f_H . The equations describing the relationships were:

$$\dot{V}_b = 248 + 1.19 (\pm 0.077) \times f_H, \quad r^2 = 0.912, \quad P < 0.001$$

and

$$V_s = 3.79 - 0.048 (\pm 0.0004) \times f_H, \quad r^2 = 0.862, \quad P < 0.001,$$

where \dot{V}_b is the cardiac output in ml min⁻¹ kg⁻¹, f_H is heart rate in beats min⁻¹ and V_s is cardiac stroke volume in ml kg⁻¹. \dot{V}_i was only weakly associated with \dot{V}_b , and reflected the change in the proportion of \dot{V}_b that supplied the ischiadic arteries.

Group II birds

Blood flows through the brachiocephalic (\dot{V}_{BCA}) and carotid (\dot{V}_{CA}) arteries were recorded from 63 dives (mean dive duration 14.4 ± 1.2 s) obtained from five ducks. Fig. 4 shows the mean blood flows through both pairs of arteries at various times during a dive. \dot{V}_{BCA} declined slightly just before a dive, but remained fairly steady until the duck surfaced, when a peak mean blood flow of 186.2 ± 8.8 ml min⁻¹ was found. \dot{V}_{CA} varied in a different manner. It rose prior to diving, then gradually declined during the beginning of a dive. Towards the end of a dive, however, it

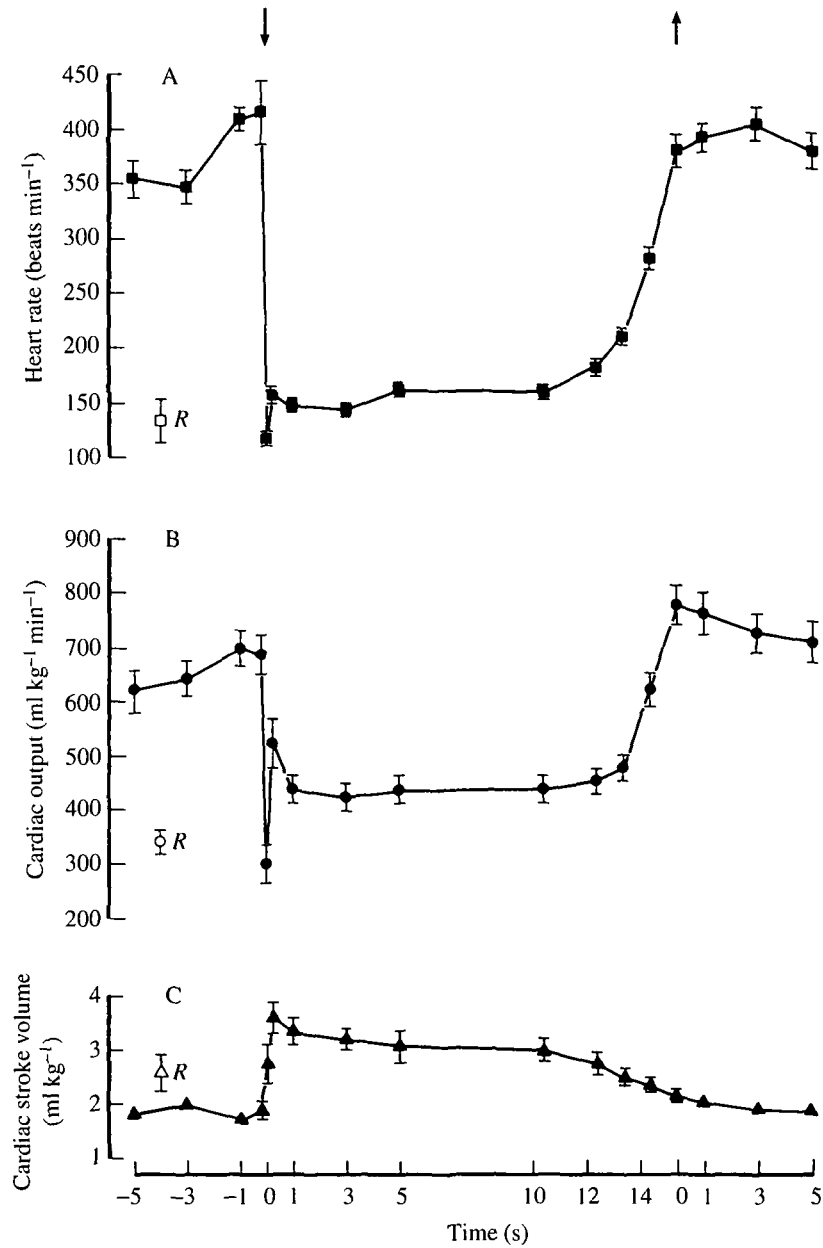


Fig. 2. Mean values (\pm s.e.) of (A) heart rate (\blacksquare), (B) cardiac output (\bullet) and (C) cardiac stroke volume (\blacktriangle) obtained from six tufted ducks during voluntary diving. The downward arrow indicates the point of submersion, the upward arrow the point of surfacing. \square , \circ and \triangle represent resting (*R*) values of above variables. Mean dive duration, 15.4 ± 1.4 s.

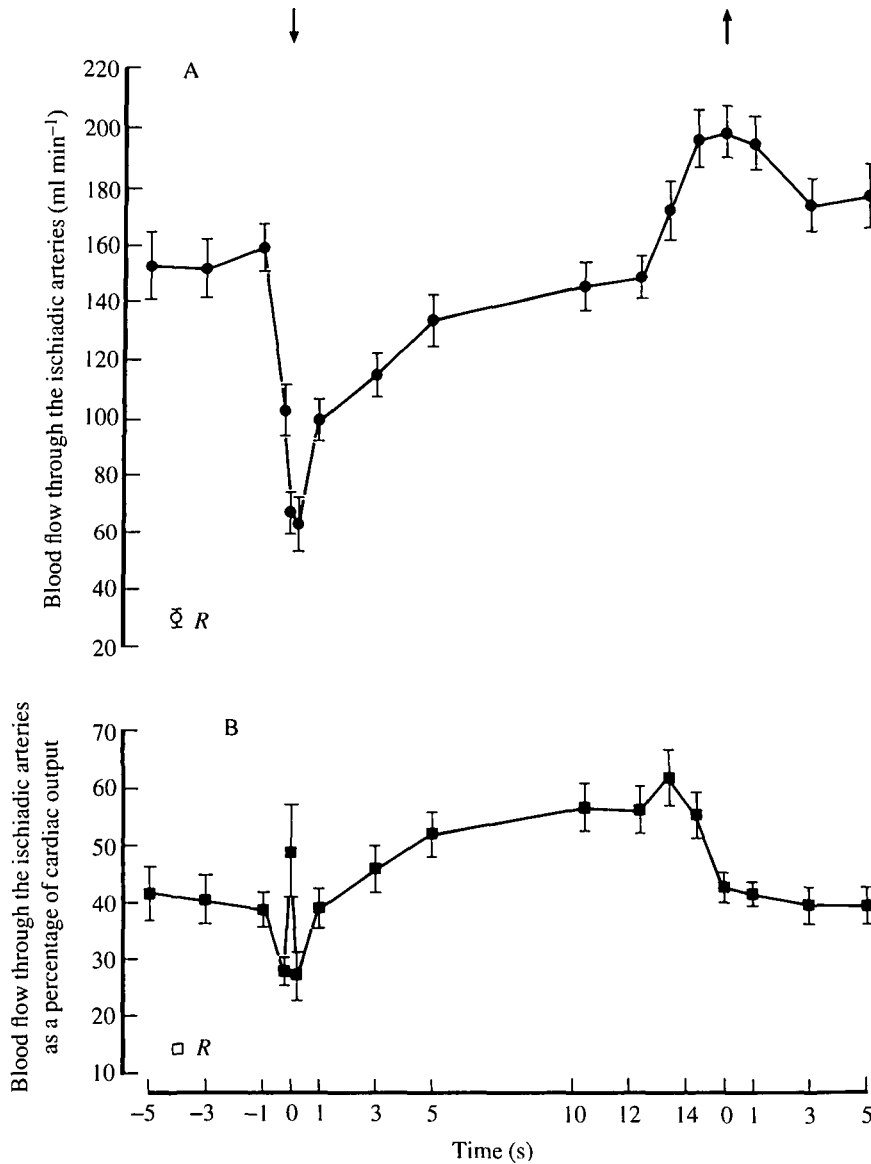


Fig. 3. Mean values (\pm s.e.) ischiadic blood flow (●) and ischiadic blood flow as a percentage of cardiac output (■) during diving in six tufted ducks. For further details see Fig. 2. ○ and □ represent resting (*R*) values of the variables.

began to increase rapidly and peaked at $151.2 \pm 7.6 \text{ ml min}^{-1}$ (3.6 times the resting level) after surfacing. The blood flow through the brachial artery (\dot{V}_{BA}) was estimated by subtracting \dot{V}_{CA} from \dot{V}_{BCA} . It would appear that \dot{V}_{BA} is a mirror image of \dot{V}_{CA} . It decreased upon diving, from the pre-dive rate of around 60 ml min^{-1} , to $14.6 \pm 1.4 \text{ ml min}^{-1}$ when the duck dived. \dot{V}_{BA} started to increase during the first few seconds of a dive towards the pre-dive level, but decreased to a

Table 1. Mean (\pm S.E.) variables measured at rest, during swimming and over the last 5 s of a dive (excluding the data obtained over the last second, when anticipatory changes may be occurring) from six tufted ducks

	Rest	Swimming	Diving
Cardiac output, \dot{V}_b (ml min ⁻¹ kg ⁻¹)	341.8 \pm 22.1	595.5 \pm 65.7*	454.2 \pm 11.6*†
Heart rate, f_H (beats min ⁻¹)	135.0 \pm 20.1	204.3 \pm 19.3*	180.3 \pm 3.6*
Stroke volume, V_s (ml beat ⁻¹ kg ⁻¹)	2.55 \pm 0.31	2.93 \pm 0.20	2.77 \pm 0.10
Blood flow through both ischiadic arteries, \dot{V}_I (ml min ⁻¹)	29.8 \pm 3.6	143.0 \pm 19.8*	153.2 \pm 4.4*
Proportion of cardiac output flowing through ischiadic arteries (%)	14.2 \pm 1.6	36.4 \pm 2.4*	57.2 \pm 2.2*†
Water speed (m s ⁻¹)	—	0.75 \pm 0.02	—
Dive duration (s)	—	—	15.4 \pm 1.4
Mass (kg)		609 \pm 7	

* represents a significant difference ($P < 0.05$) between resting and swimming or diving values; † represents a significant difference between swimming and diving.

rate of approximately 20 ml min⁻¹ over the last few seconds of a dive. This is approximately 30 % of, and significantly lower than, the resting value.

Swimming

Group I birds

Each duck was swum at speeds between 0.3 and 0.8 m s⁻¹, and readings were taken after 10–15 min at each speed. A curvilinear relationship was found between all the measured variables and swimming speed, except for cardiac stroke volume which remained reasonably constant. Fig. 5 shows the changes in \dot{V}_b , \dot{V}_I and the proportion of \dot{V}_b supplying the leg muscles at different swimming speeds. \dot{V}_b rose only slightly over the lower swimming speeds and was not significantly different from that at rest when swimming speed was 0.5 m s⁻¹. Over the higher water speeds it increased to a maximum of 634.6 \pm 97.8 ml min⁻¹ kg⁻¹ at 0.8 m s⁻¹. \dot{V}_b and V_s were again dependent on f_H , and the equations for the relationship were not significantly different from those obtained from the animals during diving. \dot{V}_I also increased as swimming speed increased (to 4.8 times the resting value), but at a faster rate than \dot{V}_b . Consequently, there was a progressive increase in the proportion of \dot{V}_b that was directed through the ischiadic arteries (Fig. 5). This proportion rose from a resting value of 14.4 \pm 1.6 % to 39.0 \pm 4.4 % at 0.8 m s⁻¹.

Group II birds

As with the birds in group I, those in group II were also swum on the water flume. f_H , as in the group I ducks, increased in a curvilinear fashion with increasing water speed. \dot{V}_{BCA} , \dot{V}_{CA} and \dot{V}_{BA} tended to decrease as the exercise intensity increased (Fig. 6) and, when swimming speed was 0.8 m s⁻¹, \dot{V}_{BA} was

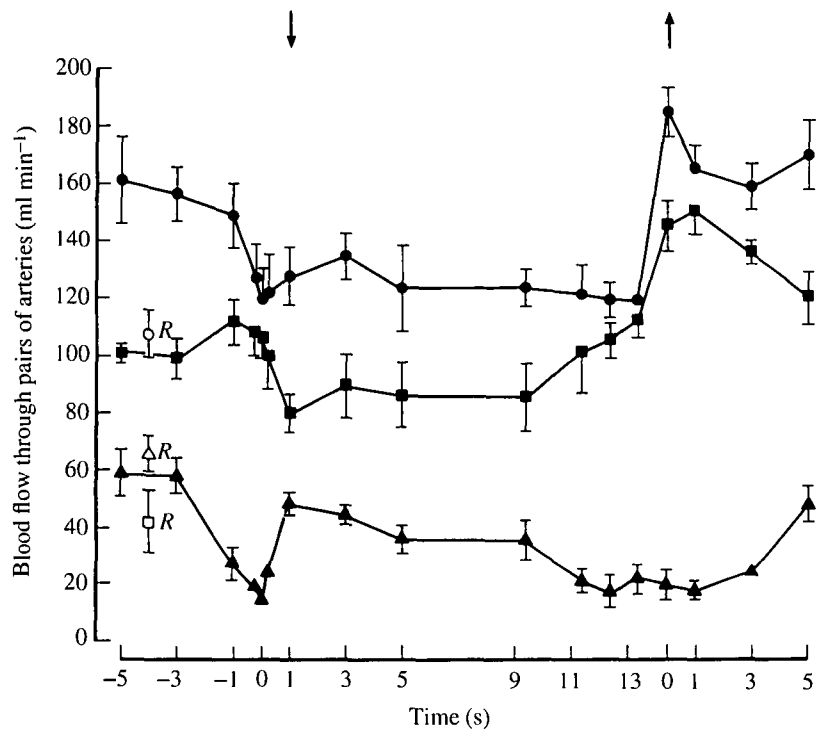


Fig. 4. Mean values (\pm s.e.) of brachiocephalic (\bullet) and carotid (\blacksquare) blood flow and estimated brachial (\blacktriangle) blood flow during voluntary diving of five tufted ducks. Brachial flows were estimated by subtracting the carotid flow from the brachiocephalic flow. The downward arrow indicates the point of submersion, the upward arrow the point of surfacing. \circ , \square and \triangle represent resting (R) values of above variables. Mean dive duration 14.4 ± 1.2 s.

$43.4 \pm 14.2 \text{ ml min}^{-1}$. This is 66% of, and significantly lower than, the resting value.

Comparison between resting, swimming and diving

Group I

A direct comparison was made between the mean resting, swimming and diving values of the different variables measured (Table 1). Mean f_H was significantly higher during both swimming and diving than it was at rest. V_S did not differ significantly between any of the conditions. Both the swimming and diving values of \dot{V}_b were significantly higher than the value at rest. However, as a result of the increased f_H and V_S during swimming, \dot{V}_b was significantly higher during this activity than during diving. Furthermore, as \dot{V}_l increased in both the swimming and diving ducks, to approximately five times the resting rate, so the proportion of \dot{V}_b that supplied the leg muscles was significantly greater at the end of a dive than it was whilst swimming at U_{\max} .

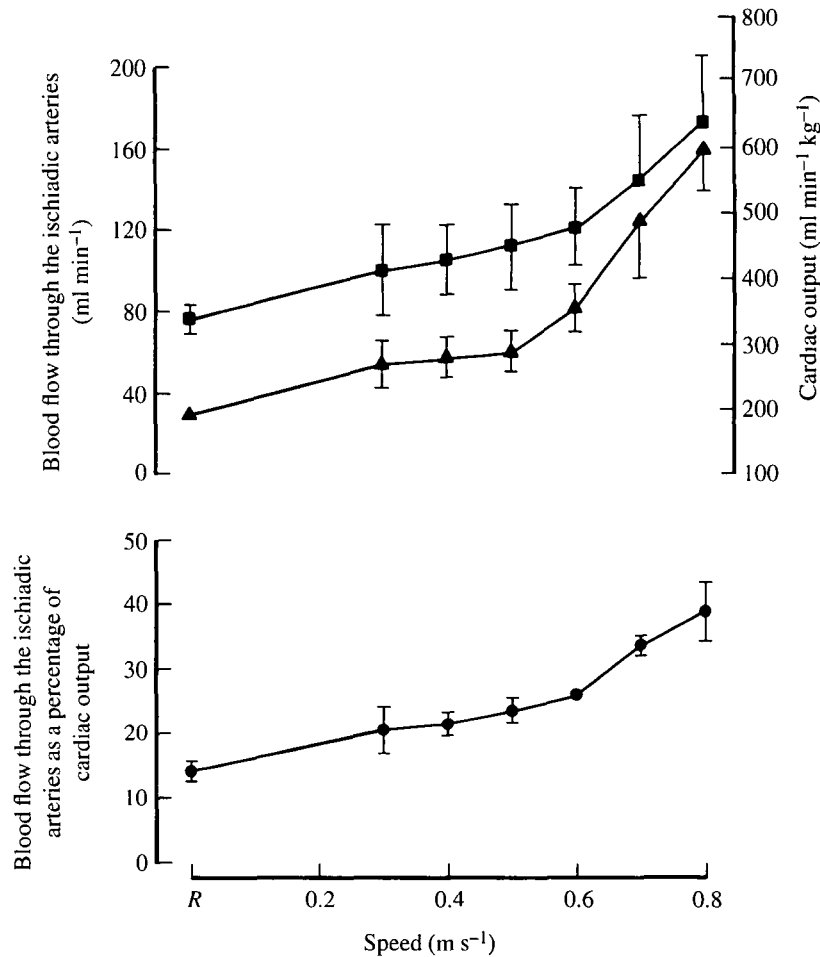


Fig. 5. Mean values (\pm s.e.) of cardiac output (■), ischiadic blood flow (▲) and ischiadic blood flow as a percentage of cardiac output (●) as a function of swimming speed. The six birds were the same as the ones used in Figs 3 and 4. R, resting values.

Group II birds

Again, the means of the different variables obtained at rest, whilst swimming and during diving were compared (Table 2). f_H during both swimming and diving was approximately 60% greater than at rest. Both \dot{V}_{BCA} and \dot{V}_{CA} during diving were significantly higher than during swimming. There was a 2.3-fold increase in \dot{V}_{CA} above the resting level during diving and this, combined with the smaller increase in \dot{V}_{BCA} , meant that \dot{V}_{BA} during the last 5 s of a dive was a significant 60% lower than that at rest. It was not, however, significantly lower than the mean \dot{V}_{BA} measured during swimming.

Discussion

The technical difficulties of recording cardiovascular variables in freely diving

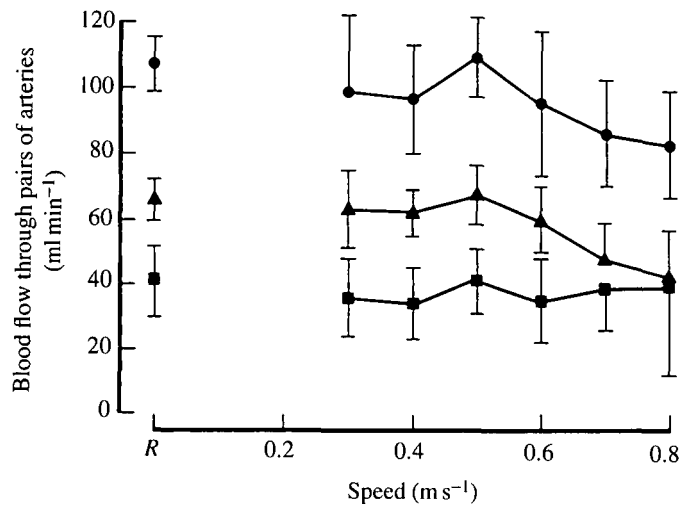


Fig. 6. Mean values (\pm s.e.) of brachiocephalic (●), carotid (■) and estimated brachial (▲) blood flows of five tufted ducks as a function of swimming speed. R, resting values.

Table 2. Mean values (\pm s.e.) of heart rate and various arterial flows during resting, swimming and diving (see Table 1) from five tufted ducks

	Rest	Swimming	Diving
Heart rate, f_H (beats min^{-1})	127.1 \pm 4.8	200.3 \pm 22.2*	203.1 \pm 14.2*
Blood flows (ml min^{-1}) through			
Brachiocephalic arteries, \dot{V}_{BCA}	107.6 \pm 8.2	84.6 \pm 10.0*	122.2 \pm 6.4*†
Carotid arteries, \dot{V}_{CA}	41.8 \pm 11.0	39.2 \pm 12.6	95.6 \pm 5.0*†
Brachial arteries, \dot{V}_{BA}	65.8 \pm 6.2	45.4 \pm 12.4*	26.6 \pm 6.6*
Water speed (m s^{-1})	—	0.74 \pm 0.03	—
Dive duration (s)	—	—	14.4 \pm 1.2
Mass (kg)		607 \pm 3	

* represents a significant difference ($P < 0.05$) between resting and swimming or diving values; † represents a significant difference between swimming and diving.

birds mean that very few studies have been performed. Only heart rate has been widely recorded, primarily because of the ease with which the electrocardiogram can be obtained by telemetry (Butler and Woakes, 1979; Kanwisher *et al.* 1981; Gabrielsen, 1985; Furilla and Jones, 1987a,b; Keijer *et al.* 1988). Only one study has measured other cardiovascular variables during voluntary diving, and this was performed on two species of penguin, *Pygoscelis papua* and *P. adeliae* (Millard *et al.* 1973). There is, therefore, very little information with which to compare the present data. Indeed, there is a paucity of data on the cardiovascular adjustments to exercise in avian species in general.

The \dot{V}_b of the ducks during rest was similar to that found in other species

(Sturkie, 1966; Jones and Holeton, 1972; Butler *et al.* 1977; Bouverot *et al.* 1979; Jones *et al.* 1979; Grubb, 1982; Kiley *et al.* 1985). However, although \dot{V}_b was lower than in previous studies on the tufted duck (Butler *et al.* 1988; Turner, 1987), V_s was similar. The higher \dot{V}_b values previously found were, therefore, due to the high f_H recorded. Over the last part of a dive, \dot{V}_b was above resting levels. This increase in \dot{V}_b is of a similar magnitude to that induced by other forms of leg exercise in birds (Bech and Nomoto, 1982; Grubb, 1982; Kiley *et al.* 1985), but contrasts with the decrease in \dot{V}_b found during involuntary submergence (Folkow *et al.* 1967; Jones and Holeton, 1972; Jones *et al.* 1979). The correlation between f_H and \dot{V}_b makes the former a very useful indicator of changes in the latter.

For most birds, there is little change in V_s when exercising (Faraci, 1986), and this was true for the swimming ducks. During diving, however, V_s varied considerably, particularly at the start of a dive. This variability of V_s during diving, compared with the constancy displayed during swimming, may have been because the diving ducks had not attained a steady state. The sudden increase in the V_s at the onset of a dive was probably due to the increased cardiac interval occurring just prior to submergence. A consequence of this would be an increase in the cardiac filling time, which in turn would cause the contractility of the heart muscle to increase. Hence, the amount of blood ejected by the heart would be elevated *via* the Frank–Starling mechanism. During involuntarily submersion of ducks the opposite occurs, V_s decreases during a ‘dive’ and increases during recovery (Folkow *et al.* 1967). This implies that there is a considerable negative inotropic effect due to increased vagal activity during involuntary ‘dives’ (Folkow and Yonce, 1967), causing a reduction in stroke volume despite the increase in central venous pressure (Folkow and Yonce, 1967).

The irregularities seen on the ischiadic blood flow trace were probably caused by contractions of the muscles surrounding the vascular bed supplied by the artery. Comparable fluctuations in flow have been reported in the vessels supplying the human quadriceps during rhythmic exercise (Walloe and Wesche, 1988). Mean \dot{V}_l increased approximately fivefold above resting levels during both diving and high-speed swimming in the tufted duck. Similar increases in the blood flow to the leg were found in the Pekin duck during running (Bech and Nomoto, 1982), the tufted duck during swimming (Butler *et al.* 1988) and during electrical stimulation of the leg muscles of the duck (Folkow *et al.* 1966). This response (an increase in blood flow to the leg) contrasts sharply with what is seen during involuntary submersion, where the blood flow to the leg falls dramatically (Folkow *et al.* 1966; Butler and Jones, 1971). In the voluntarily diving penguin, the blood flow in the femoral artery also decreases (Millard *et al.* 1973), but this is not altogether surprising as the penguin propels itself through the water using the pectoral muscles and not those of the leg. The effect being monitored by Millard *et al.* (1973) was probably a redistribution of blood flow from the inactive (leg) to the active (wing) muscles, a situation analogous to the responses occurring in the diving ducks.

The continual increase in ischiadic blood flow throughout diving in the tufted duck may seem peculiar since there is probably a reduction in the work that the leg

muscles have to perform during the later stages of a dive. This is because the initial part of the dive includes the work needed to descend through the water column and the possibility of a reduction in buoyancy through air loss from between the feathers as the dive progresses. In addition, the oxygen consumption of the ducks appears to decrease as a dive progresses (Bevan *et al.* 1992), indicating that the oxygen requirement is also reduced. It might be expected, therefore, that the ischiadic blood flow during a dive would stabilise or even decrease. However, as the oxygen content of the blood will also decrease during a dive, an increase in perfusion will be necessary to transport adequate oxygen to the contracting muscles.

Since the proportional increase in \dot{V}_i is greater than the proportional increase in \dot{V}_b during swimming and diving, a redistribution of blood flow must be occurring. Butler *et al.* (1988) found that there was a redistribution of blood flow in the swimming tufted duck away from the inactive flight muscles. It was suggested by these authors that the same response might occur during voluntary submersion, but that the redistribution would be even greater. This prediction is confirmed by the significantly greater proportion of \dot{V}_b being directed to the legs during diving than during swimming.

Ideally, the blood flow along the brachial artery should have been measured directly, but this was not possible because of the numerous small branches arising from it. These small arteries were traced in a number of birds and were found to supply the supracoracoideus muscle and the skin surrounding the breast muscle. The estimated brachial blood flow in the present study, therefore, not only perfused the flight muscles, but a small fraction also perfused the skin. There was no way of differentiating between the two, but it was assumed that the blood flow to the skin would be quite small during diving.

The \dot{V}_{BA} whilst swimming at top speed was significantly lower than that at rest, agreeing with the study of Butler *et al.* (1988). As the pectoral muscles of birds can make up between 10 and 25% of the body mass (Bethke and Thomas, 1988; Turner and Butler, 1988) and are inactive during swimming and diving, in ducks at least, they represent a large reserve from which blood flow can be diverted. The reduction in blood flow to these muscles during exercise is, therefore, not surprising. In the diving bird, there was an even greater reduction in \dot{V}_{BA} , supporting the idea that a more intense peripheral vasoconstriction occurs in the inactive muscles during diving than during swimming (Butler, 1982; Woakes and Butler, 1983; Butler *et al.* 1988).

The \dot{V}_{CA} during swimming was unchanged from the resting level, which is unlike the response in the walking duck, where a 2.3-fold increase was found (Bech and Nomoto, 1982). The latter was probably a thermoregulatory mechanism that would be unnecessary for a swimming bird, where heat dissipation is not a problem.

In spite of the reduction in the perfusion of the flight muscles, there was no net redistribution from the brachiocephalic artery during diving, as \dot{V}_{CA} increased twofold. The considerable increase in \dot{V}_{CA} could have resulted from a number of

Table 3. *Estimated blood flow available to the body tissues, excluding the flow through the ischiadic and brachiocephalic arteries, in tufted ducks at rest, during swimming close to maximum sustainable speed and during diving for approximately 15 s*

	Rest	Swimming	Diving
Cardiac output (ml min ⁻¹)	208	363	277
Blood flow through ischiadic arteries (ml min ⁻¹)	30	143	153
Blood flow through brachiocephalic arteries (ml min ⁻¹)	108	85	122
Blood flow available to rest of body (ml min ⁻¹)	70	135	2

Data from Tables 1 and 2.

factors. First, the ducks, when diving, were actively searching for food. To do this, the muscles of the neck were used to move the head from side to side. Second, the ducks continuously pecked at food particles in the water, so the mandibular muscles were also working. A third possibility is that the ducks were more alert than when at the surface. In humans, any increased mental activity is matched by an increase in the cerebral blood flow (Heistad and Kontos, 1983). A similar mechanism may have been working in the ducks. Last, but certainly not least, as the oxygen content of the blood will decrease during a dive, an increase in blood flow will be necessary to maintain the oxygen supply to the brain, given that it has to derive all its energy aerobically (cf. *V_I*).

If the blood flow along the brachiocephalic and ischiadic arteries are subtracted from cardiac output, it can be seen that, during diving, there is very little blood flow available to the rest of the body (Table 3). It should be noted that the figures for the blood flow to the rest of the body are only an indicator of what is available and should not be taken as being exact, since the figures are derived from different animals (see Tables 1 and 2 for original values). Nevertheless, other vascular beds, as well as the inactive flight muscles, must have had a reduced blood supply during diving compared with that during swimming or while the birds were at rest. During swimming, it has been found that the blood flow to the gastrointestinal tract as a whole is unaffected by exercise; but certain areas have a reduced flow (Butler *et al.* 1988). However, even though diving is primarily a foraging activity, the birds may only gather food and store it in the crop during the diving bouts, waiting until a bout is over before digesting the food. In this case, there would be no need for any appreciable blood flow to the gastrointestinal tract. Indeed, prolonged periods of crop distension may be involved in a reflex suppression of feeding (Hodgkiss, 1981). A full crop may, therefore, be the stimulus to end a diving bout. Another tissue having a reduced blood flow would be the respiratory muscles, as they are probably inactive during submersion.

It would have been interesting to measure the blood flows over the later stages

of dives of long duration (>35 s), when the heart rate starts to fall (Stephenson *et al.* 1986; Bevan *et al.* 1992), and during 'enclosed' dives, when an abrupt drop in heart rate occurs (Stephenson *et al.* 1986). What happens to the blood flow to the leg during these periods, when there is probably a reduction in cardiac output, is not yet known. If the emphasis during these dives is placed on the conservation of oxygen for the oxygen-dependent tissues, then even the blood flow to the active leg muscles will presumably decline. Involuntary submersion of the Pekin duck, *Anas platyrhynchos*, causes a decline in the tension produced by the stimulated tibialis anterior muscle (Jones *et al.* 1988). This would probably also occur in the active leg muscles of a voluntarily diving tufted duck if an intense peripheral vasoconstriction were invoked.

This study is the first to measure directly cardiac output and regional blood flow in a voluntarily diving bird. It shows that, despite a lower cardiac output, the blood flow to the active leg muscles during diving is equivalent to that whilst the duck is swimming on the surface at U_{\max} . The reduced brachial blood flow shows that a redistribution of blood away from the inactive flight muscles does occur during swimming and diving, but that, in the diving tufted duck at least, vasoconstriction must also be occurring in other vascular beds.

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