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BLOOD FLOW DISTRIBUTION IN SUBMERGED AND SURFACE-SWIMMING DUCKS

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Summary

Observations that the response of the avian heart rate to submergence varies under different circumstances have led to speculation about variability of blood flow distribution during voluntary dives. We used a radiological imaging technique to examine the patterns of circulating blood flow in captive redhead ducks (*Aythya americana*) during rest, swimming, escape dives, forced dives and trapped escape dives and have shown that blood flow distribution in escape dives was the same as that in ducks swimming at the water surface. The response during trapped escape dives, however, was highly variable. Blood pressure was unchanged from the resting value during all activities. Predictions made about blood flow distribution during unrestrained dives on the basis of heart rate and other indirect data were confirmed in this study. However, the trapped escape dive responses indicated that heart rate alone is not always a reliable indicator of tissue blood flow in exercising ducks.

Introduction

The development of small radiotelemetry devices in the 1970s allowed, for the first time, direct physiological observations to be made in voluntarily diving birds. It soon became apparent that the marked fall in heart rate (the 'diving bradycardia') that is characteristic of the oxygen-conserving response to forced dives (manual immersion of the head) is either less pronounced or absent during voluntary dives (Millard *et al.* 1973; Butler and Woakes, 1979; Kanwisher *et al.* 1981). Recent research using diving ducks has demonstrated that heart rate varies considerably during different kinds of unrestrained dives (Stephenson *et al.* 1986; Furilla and Jones, 1987). The assumption that heart rates measured using telemetry can reliably predict other aspects of the circulatory response has formed the basis of hypotheses concerning the nature and role of the peripheral

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circulatory adjustments during different voluntary and involuntary diving activities.

It has been proposed (Millard *et al.* 1973; Butler, 1982) that the cardiovascular adjustment made by birds undertaking voluntary dives (which entail exercise combined with breath-hold) are a composite of the usual exercise response, which involves increased cardiac output and redistribution of blood flow in favour of the exercising skeletal muscles (Butler *et al.* 1988), and the forced dive response, in which hypoxia-tolerant tissues, including the skeletal muscles, are rendered ischaemic (Johansen, 1964; Butler and Jones, 1971; Jones *et al.* 1979; Heieis and Jones, 1988). This raises a question about blood flow in the locomotory muscles during active unrestrained dives: do these muscles receive a reduced blood supply, as in the forced dive response, or are they continuously perfused, as during surface swimming?

The following observations have led to the prediction that the legs will be continuously perfused during voluntary dives (Eliassen, 1960; Butler, 1982; Stephenson and Jones, 1989): (1) voluntary dives are of short duration (Dewar, 1924); (2) heart rate and oxygen consumption are well above resting levels in voluntarily diving ducks (Woakes and Butler, 1983); (3) the active leg muscles must generate considerable power output to overcome the buoyant force of the submerged birds (Stephenson *et al.* 1989*a*; Lovvorn *et al.* 1991); and (4) there is only a small amount of stored oxygen bound to myoglobin (Keijer and Butler, 1982; Stephenson *et al.* 1989*b*).

It has been shown that, under circumstances where ducks are temporarily unable to regain access to the water surface at the end of otherwise normal voluntary dives, their heart rate falls dramatically as soon as they become aware of the situation (Stephenson *et al.* 1986; Furilla and Jones, 1987). Assuming that blood pressure is maintained at normal levels, the occurrence of a bradycardia under these circumstances leads to the prediction that the peripheral vascular resistance must increase considerably and may cause a reduction of blood flow to the active leg muscles.

We have addressed these questions by using a radiological imaging technique to observe directly the distribution of cardiac output to different parts of the body in the redhead duck (*Aythya americana*). We compared blood flow distribution in the birds at rest, while swimming vigorously at the water surface and during three types of dive: forced, escape and trapped escape dives. In the escape and trapped escape dives, birds were unrestrained but confined. In forced dives, birds were restrained and only the head was submerged.

Materials and methods

Eleven redhead ducks, *Aythya americana* Eyton, of either sex, were used in this study. Mean (±S.E.M.) body mass was 0.974±0.011 kg. They were kept on an outdoor diving pond and fed high-protein growers pellets and mixed grains *ad libitum*. A sterile PVC cannula (0.58 mm i.d, 0.99 mm o.d.; Bolab Inc., Lake

Havasu City, Arizona) was inserted into one brachial artery under local anaesthesia (1 % lidocaine HCl, subcutaneous injection; Xylocaine, Astra Pharmaceuticals Canada Ltd, Mississauga, Ontario, Canada) and advanced until the tip lay in the left ventricle, as indicated by the blood pressure record. The cannulae were pre-treated with TD–MAC heparin complex (Polysciences Inc., Warrington, Pennsylvania) to inhibit blood clotting, and they were flushed daily using heparinized sterile saline (50 USP units heparin ml^{-1}; Allen and Hanburys, Toronto, Ontario, Canada). The sutured skin was dusted with a neomycin sulphate/amino acid antibiotic powder (Cicatrin, Burroughs Wellcome Inc., Kirkland, Quebec, Canada) and the ducks were subsequently given daily injections (125 mg kg^{-1} intramuscularly) of ampicillin sodium (Penbritin; Ayerst Laboratories, Montreal, Quebec, Canada). All procedures were approved by the Animal Care Committee of the University of British Columbia and were performed in accordance with the guidelines laid down by the Canadian Council on Animal Care. The ducks were allowed at least 24 h to recover before being used in experiments.

Observations were made during the following types of behaviour: resting, in which the ducks were allowed to sit in a quiet, dark box for at least 30 min before measurements were made; swimming, in which the ducks were made to swim at a velocity of 0.7 m s^{-1} (close to their maximum sustainable swimming speed) on the surface of a water flume; escape dives, in which ducks were placed on an uncovered outdoor pond and induced to dive on sight of a hand-held net; trapped escape dives, in which ducks were placed on a covered tank, induced to dive as above, and then prevented from resurfacing for up to 60 s by closing a trapdoor over the water surface; and forced dives, in which the head of a restrained duck was manually immersed in water for approximately 60 s. Each duck was injected with blood flow tracer on up to four separate occasions, each one during a different randomly selected behaviour. Thus, none of the ducks was measured in all behavioural categories.

Early attempts to train the ducks to carry a small (80 g) infusion pump in the form of a backpack were unsuccessful so we resorted to the use of a 4 m long cannula for injection of the blood flow tracer and for recording ventricular pressure during escape dives and trapped dives. A shorter cannula (<1 m) was used at other times. For each behavioural category, heart rate was calculated from the left ventricular pressure trace and a 'snapshot' of the distribution of blood around the systemic circulation was obtained by injection of a suspension of macro-aggregated albumin particles labelled with the gamma-emitting isotope technetium-99m (^{99m}Tc-MAA). Upon injection, ^{99m}Tc-MAA was distributed around the body in proportion to blood flow and trapped in the capillary beds of perfused tissues.

Each duck was injected with 200 μl of ^{99m}Tc-MAA suspension, containing 2×10^5 particles. This was washed in with 1 ml of 0.8 % saline at room temperature. Control injections of saline had no consistent or marked effects on heart rate or peak ventricular blood pressure. Injections occurred under steady-state conditions

during resting and swimming, after 1 s of immersion during escape dives, after 33±8 s of immersion during forced dives and after 39±5 s of immersion during trapped escape dives. Injection time was approximately 2–3 s. The total activity of the tracer at the time of injection was approximately 60–100 MBq kg^{-1}. Particle diameter, measured against a 50 μm grid from photographic records, averaged 30–40 μm. Unlike glass microspheres, ^{99m}Tc-MAA particles are virtually neutrally buoyant in physiological saline and, since the suspension does not settle rapidly, there is no need for vigorous mixing right up to the moment of injection. In the escape dive and trapped escape dive experiments the suspension was mixed and then advanced into the long cannula until it was close to the duck, thereby reducing injection time and volume. ^{99m}Tc-MAA suspension was prepared using a commercially available kit (Frosstimage MAA, Merck Frosst Canada Inc., Kirkland, Quebec, Canada). The ^{99m}Tc generator consists of a column of molybdenum-99 (^{99}Mo) adsorbed onto alumina. ^{99}Mo decays to ^{99m}Tc with a physical half-life of 66 h and sodium pertechnetate was produced each day by elution of the column with 0.9 % NaCl solution. This eluate was added to the MAA vial to produce ^{99m}Tc-MAA suspension containing 10^6 particles ml^{-1} and an initial activity of approximately 700 MBq ml^{-1}. Less than 1.5 % of the label was unbound. ^{99m}Tc decays to ^{99}Tc by isomeric transition with a physical half-life of 6.02 h and was therefore freshly prepared each day.

After injection of the ^{99m}Tc-MAA suspension, the ducks were captured and immediately transported to the Department of Nuclear Medicine, University Hospital, Vancouver, to be imaged. Ducks were taped to a circular plastic plate ventral side down and imaged. They were then turned left lateral side down and imaged again. Scan time was approximately 15 s per image and data were acquired using an Orbiter 3700 Digitrac gamma-sensitive camera, interfaced with a microprocessor-controlled image analyser (MicroDelta Plus) using 'Clinic' version 7.1 software (Siemens, Toronto, Ontario, Canada). The resolution of the system was 2 mm and the average image size was 13 219 pixels. The colour-enhanced digital images, displayed on the computer monitor, were divided (using the above software) into various anatomical regions, of which the following were subsequently analysed: whole body, hindlimbs, brain and heart. The ventral images provided a larger surface area and therefore better resolution so these were used in all quantitative analyses. The hindlimbs, which had been pulled laterally away from the body during imaging, as well as the heart and brain were always clearly visible and were outlined by eye as accurately as possible. Repeated analyses of one image indicated an acceptably low level of variability between analyses (coefficients of variation [(S.D./mean)×100] (N=4) were: whole body, 0.08 %; brain, 0.2 %; heart, 0.1 %; legs, 0.6 %), confirming the validity of this approach.

Ratios of regional count/whole-body count were obtained and analysed statistically following Zar (1984). Since the sample sizes were small, nonparametric tests were used. For multi-sample analyses, the Kruskal–Wallis test was used and for two-sample analyses the Mann–Whitney test was employed. Results were considered significant at the 95 % confidence level (P<0.05).

Results

The fully analysed images provided an approximation of the regional blood flow in terms of the percentage of cardiac output which perfused each region at the time of injection. Fig. 1 demonstrates clearly that blood flow distribution differed considerably between behaviours. Summary statistics are presented in Table 1. The number of measurements made using each duck depended upon its tolerance of handling and on the condition of the ventricular cannula. The cannula often became blocked or was ejected from the left ventricle during experiments, which further reduced the success rate. Since availability of these captive wild ducks was limited, sample sizes were unavoidably smaller than we would have liked them to be.

Measurements were made in five ducks under 'resting' conditions but we were confident that just three of these were inactive and undisturbed, so only these were included in Table 1. Their blood flow pattern is illustrated in Fig. 1A. The other two ducks were agitated by the cannula and persistently pecked at it. Heart rate was higher in the latter ducks (288 and 315 beats min^{-1}) at the time of tracer injection but relative blood flow to the heart and hindlimbs was the same as in the other inactive ducks. Relative blood flow to the brain was very similar in the three inactive ducks (Table 1), but was slightly more variable in the two restless ducks (1.6% and 5.6% in the latter). Relative blood flow to the heart was statistically the same in all behaviours.

There was an unmistakable oxygen-conserving response in three ducks during forced dives (Fig. 1C): compared with the resting ducks, a significantly larger proportion of the cardiac output went to the brain and there was a non-significant reduction in relative blood flow through the legs (Table 1). Pre-submergence heart rate was 147±12 beats min^{-1} (N=3) and it decreased to approximately 37% of this value during head immersion (55±4 beats min^{-1}). A fourth duck exhibited a tachycardia rather than the normal bradycardia and was excluded from the

Table 1. *Cardiovascular responses of redhead ducks (*Aythya americana*) to resting, swimming, forced dives and escape dives*

Behaviour	Heart rate (beats min^{-1})	Relative blood flow (%)		
		Brain	Heart	Hindlimbs
Resting	148±2 (3)	2.4±0.1 (3)	12.8±2.0 (3)	17.5±3.7 (3)
Swimming	243±21 (4)*	2.7±0.2 (4)	8.9±0.6 (4)	37.9±2.0 (4)*
Forced dive	55±4 (3)*	11.1±2.5 (3)*	12.2±2.2 (3)	11.6±3.3 (3)
Escape dive	246±27 (3)*	3.7±0.5 (5)	8.3±0.7 (5)	38.0±2.9 (5)*

Mean values±S.E.M. are given with sample size (number of animals) in parentheses.

Asterisks refer to values which differ significantly (at the 95% confidence level) from the resting value within a column.

Relative blood flow refers to the percentage of cardiac output which perfused the named organs at the time of injection.

Fig. 1. Ventral images of ^{99m}Tc-MAA distribution in the tissues of redhead ducks (*Aythya americana*) during various activities. The vertical colour bar indicates relative activity (equivalent to relative blood flow) where white is high and purple is low activity. The images indicate regional distribution of blood flow as a proportion of cardiac output at the time of injection. (A) Rest; (B) swimming; (C) forced dive; (D) escape dive; (E, F) trapped escape dives. The two trapped escape dive images illustrate the variability of this response. Two other trapped dives were qualitatively similar to F.

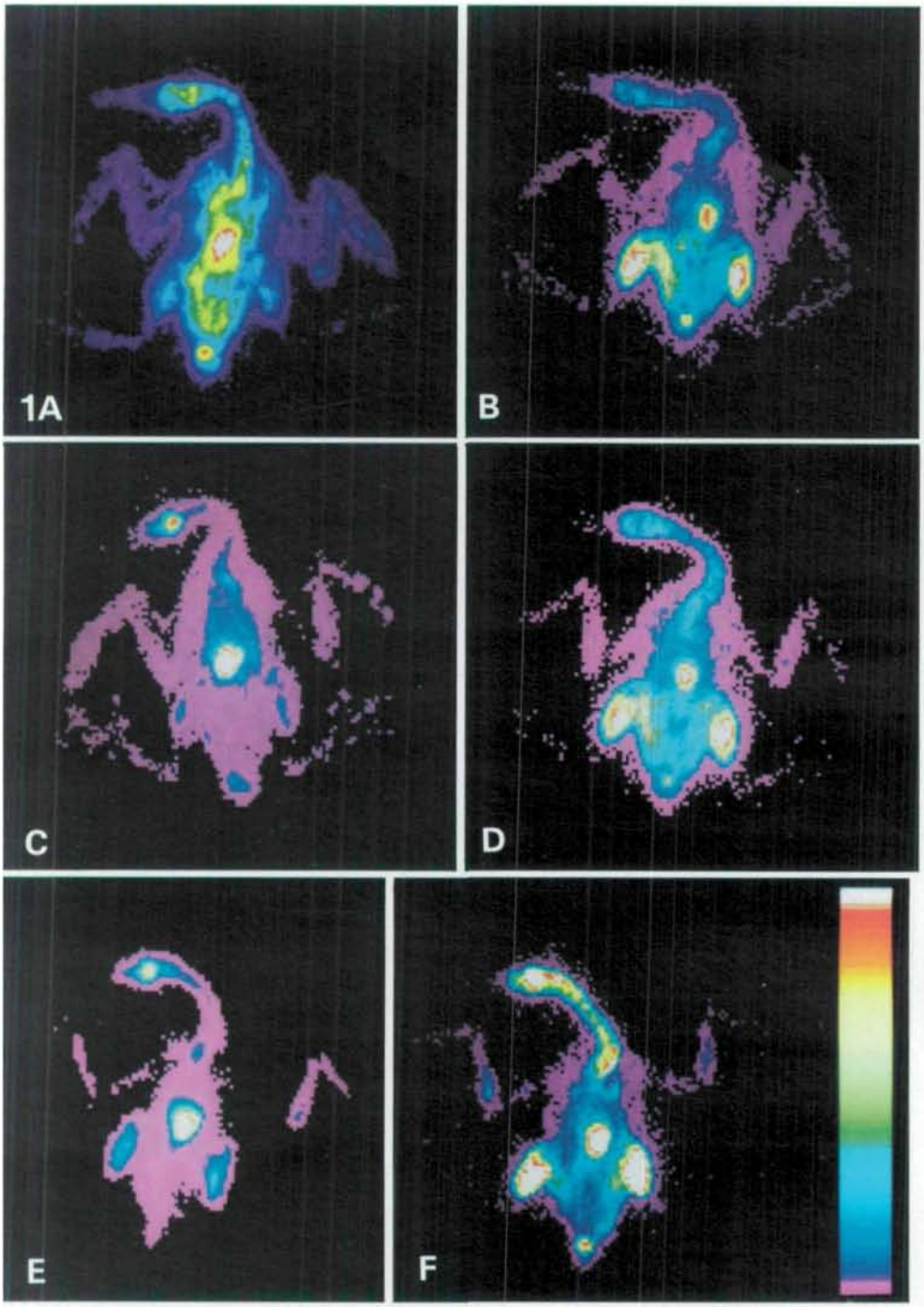
analysis (Table 1) although its blood flow pattern was qualitatively similar to those of the other three ducks.

During vigorous surface swimming all four ducks tested responded with a significantly increased perfusion of the working leg muscles compared with resting ducks (Table 1, Fig. 1B). Relative blood flow to the brain and heart was unchanged from the resting value. During swimming, heart rate was approximately 1.6 times the resting value.

Heart rate during escape dives was significantly elevated above the resting level and was similar to that during surface swimming (Table 1). It can be seen in Fig. 1B,D and in Table 1 that the pattern of blood flow in escape dives was also closely similar to that during surface swimming, with a significantly increased relative hindlimb blood flow compared with resting ducks. The duration of escape dives was 5±0.6 s (N=5).

The results of the trapped escape dive experiments were more equivocal. Both the heart rate responses and the blood flow patterns were highly variable, as shown in Fig. 2. Four ducks were tested successfully and only one of these exhibited an oxygen-conserving response similar to that observed during forced dives (Figs 1E and 2, duck 4). In this duck, heart rate decreased by 77 % and relative blood flow to the brain and hindlimbs (Fig. 2, 9.9 and 13.9 %, respectively) resembled those in forced diving ducks. However, relative blood flow to the heart was higher (24.4 %) in this trapped escape diving duck than in the forced diving animals. In the other three trapped diving ducks (Fig. 2, ducks 1–3), blood flow was redistributed in a pattern more closely resembling that observed in swimming and escape diving ducks (compare Fig. 1F with 1B and 1D) with a high relative hindlimb blood flow. Relative blood flows to the brain and heart were variable during trapped escape dives and they were not correlated with submergence time, dive heart rate or the difference between pre-dive and dive heart rates. Heart rates were high in all four ducks while the ducks were preparing to evade the net before trapped escape dives (370±32 beats min^{-1}), and the decreases in heart rate during trapped escape dives ranged from 7 to 81 % of the pre-dive value (Fig. 2).

Peak left ventricular blood pressure was 23.5±2.2 kPa in the resting ducks and did not change significantly during swimming (24.5±1.2 kPa), forced dives (22.2±2.2 kPa), escape dives (20.6±0.6 kPa) and trapped escape dives (21.7± 0.6 kPa). However, we are cautious about interpreting the pressure trace during unrestrained dives (escape and trapped escape) because in most cases a significant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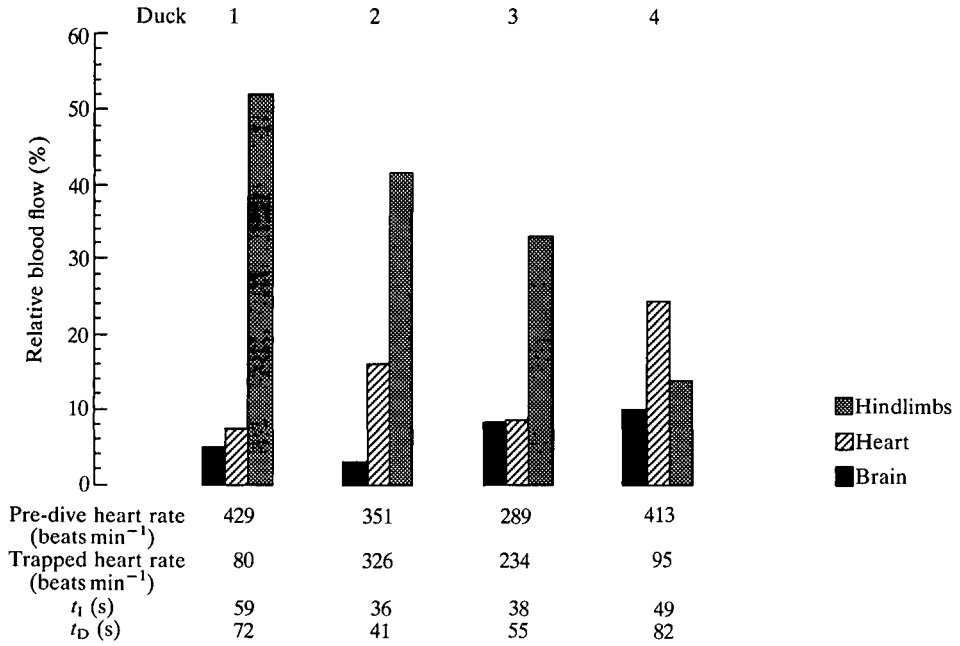

Fig. 2. Cardiovascular responses of four redhead ducks (labelled 1–4) during individual trapped escape dives. In each case the duck was induced to dive on sight of a hand-held net and then access to the water surface was prevented by a trapdoor. The total dive time (t_D) and the time to tracer injection (t_I) are shown below each group of bars. Relative blood flow represents the percentage of cardiac output which perfused the brain, heart and hindlimbs at the time of injection of the ^{99m}Tc-MAA suspension. The heart rates of each animal before the dive (pre-dive) and during the trapped part of the dive (trapped) are also given below each group of bars.

amount of noise was generated by movement of the cannula and peak pressure was often not reliably recorded. Furthermore, the 4 m cannula may have led to an underestimate of systolic pressures as a result of an increased time constant in the system. Recordings were also made during two escape dives and three trapped escape dives in which the cannula had withdrawn from the ventricle into the proximal aorta and in these cases there was no change in mean arterial blood pressure during the dives (24.7±0.7 kPa in escape dives and 17.8±2.2 kPa in trapped escape dives).

Discussion

In general, heart rate, blood pressure and relative blood flow measured in resting, swimming and forced diving ducks corroborated the findings of previous studies in ducks (Johansen, 1964; Jones *et al.* 1979; Butler *et al.* 1988; Heieis and Jones, 1988). The ^{99m}Tc-MAA imaging technique provided a clear visual demonstration that perfusion of the active hindlimb muscles increased during surface

swimming (Fig. 1B), confirming the work of Butler *et al.* (1988). It also clearly illustrated that blood flowed preferentially to the brain during forced head submersion in diving ducks (Fig. 1C), as has been shown in dabbling ducks (Heieis and Jones, 1988). However, the blood flow redistribution during forced dives was less pronounced in the present study than has been reported previously (Johansen, 1964; Jones *et al.* 1979), possibly because of the shorter immersion times used here (time to tracer injection, t_I=33±8 s; total immersion time, t_D=70±7 s).

All aspects of the cardiovascular response were the same in escape dives and during surface swimming. The heart rate response to escape dives was found to be the same as that reported during voluntary feeding dives in this species (Furilla and Jones, 1987), confirming similar observations in the tufted duck (Butler and Woakes, 1979). We have also confirmed that arterial blood pressure is maintained close to pre-dive levels in diving ducks, despite the sudden marked changes in heart rate at the onset of the dives (Jones *et al.* 1988). This contrasts with the observation that blood pressure increased in freely exercising penguins (Millard *et al.* 1973). It would appear, therefore, that during unrestrained dives, when the ducks are not trapped or held underwater and are therefore able to determine the duration of breath-hold, their cardiovascular systems adjust in such a way as to facilitate oxygen transport to the actively working muscles, supporting previous predictions based on analyses of heart rate, energetics and behaviour (Eliassen, 1960; Butler, 1982; Stephenson and Jones, 1989). The escape dives recorded in this study (5 s duration) were shorter than the feeding dives observed previously (approximately 10–20 s; Dewar, 1924; Furilla and Jones, 1986), but natural escape dive durations have not been reported. Feeding dive duration is dependent upon water depth in these benthic-feeding birds (Dewar, 1924) but it is not known whether the same holds true for escape dives.

It has been reported that the response to being trapped under water consists of an immediate and pronounced reduction in heart rate (identical to that seen during forced dives), which begins when the ducks first appear to become aware of their situation (Stephenson *et al.* 1986). However, the ducks in the present experiments were induced to dive before being trapped, rather than finding themselves trapped at the end of an otherwise normal feeding dive. In this case the heart rate response was much more variable. Stephenson (1987) also observed a more variable and usually less intense heart rate response during trapped escape dives, compared with trapped voluntary dives, in the tufted duck. It can be seen in Figs 1E,F and 2 that the blood flow distribution pattern was variable too. Of the four trapped dives in which both heart rate and blood flow distribution were successfully observed, only one (Figs 1E and 2, duck 4) had a very pronounced reduction in flow to the legs, that is, it showed the predicted oxygen-conserving response seen during forced dives. All of the other ducks had heart rate and blood flow patterns which were more similar to the escape dive and swimming responses (Figs 1F and 2, ducks 1–3). It is worth noting here that the cannula of the duck showing the oxygen-conserving response (Fig. 1E) had become caught around a vertical standpipe in the tank during injection of the ^{99m}Tc-MAA suspension. The

duck struggled to free itself but its level of physical activity may not have been the same as that of the other trapped diving ducks. It is also possible that additional arousal contributed to the onset of the oxygen-conserving cardiovascular response in this case. There was no correlation between heart rate and relative blood flow during trapped escape dives, highlighting the fact that heart rate alone is not a completely reliable predictor of changes in tissue blood flow.

In this study, the trapped ducks continued to swim under water for up to a minute without invoking a deep bradycardia, in sharp contrast with most previous observations (Stephenson *et al.* 1986; Furilla and Jones, 1987), where the onset of bradycardia was virtually instantaneous once the ducks became aware of their plight. Perhaps the less intense response during trapped escape dives, as opposed to trapped voluntary dives, represents a physiological compromise between saving oxygen for the heart and brain, while retaining the capacity to swim in order to find an escape route. Certainly, the hindlimbs were observed to fatigue much more rapidly in ducks which had a pronounced bradycardia (Stephenson *et al.* 1986; Furilla and Jones, 1987) and it has been shown that the myoglobin-bound oxygen store in these birds is sufficient to support no more than a few seconds of diving exercise (Keijer and Butler, 1982; Stephenson *et al.* 1989*b*). It has been reported that the carotid body chemoreceptors are partly responsible for the decline in heart rate during long-duration feeding dives and trapped voluntary dives (Butler and Woakes, 1982; Butler and Stephenson, 1988). However, in the present study, the two longest trapped escape dives elicited very different responses (Fig. 2, ducks 1 and 4), suggesting that factors other than chemoreceptor input are important during prolonged trapped escape dives.

The technique used to measure blood flow in this study has several advantages over other commonly used methods. ^{99m}Tc decays with a half-life of 6.02 h and the MAA particles are effectively destroyed within 24 h. Control experiments were performed in which two ducks were injected and then imaged after 1 and 25 h. The residual activity was very low in the second image ($\leq$3 % remaining) and was located mainly in the abdomen, with approximately 50 % of the residual counts located in the region of the liver. According to Merck Frosst Canada Inc., MAA is fragile and the particle size is eroded by fragmentation. MAA is cleared from human lung capillaries with a half-life of approximately 2–3 h and the fragments are accumulated by the reticuloendothelial system. This appears to take place primarily in the liver in the ducks used in this study. Another practical advantage lies in the fact that the particles settle very slowly after mixing, making injections relatively easy. Thus, unlike the radioactive glass microsphere technique, the tracer can be mixed prior to, rather than simultaneously with, the injection. In addition, the image is obtained non-invasively so the animal does not need to be killed for a measurement to be made, and the tracer is rapidly metabolised so that, in principle, several measurements can be made in the same individual, an important consideration in experiments such as this one in which the animals are not domesticated and may therefore be in short supply. It would have been statistically advantageous to have had larger sample sizes, but this could not be

achieved because the number of successive measurements was limited by the tolerance of the ducks to repeated handling and to the presence of the cannula in the left ventricle. For this reason, none of the ducks was subjected to more than four experiments in this study, some of which were unsuccessful.

The main disadvantage of the method is its inability to determine blood flow in absolute units. The images are two-dimensional and cannot, therefore, be resolved in the vertical plane. Taking lateral and ventral images from the same duck allowed us to interpret our results with more confidence but we could still only quantify blood flow directly in terms of organ to whole-body ratios. The changes in relative blood flow are only meaningful when interpreted in the light of concurrent changes in heart rate or, preferably, cardiac output. Thus, an increase in the relative blood flow to an organ may not represent an increase in absolute flow if it is accompanied by a decrease in heart rate (e.g. as occurs in the brain during forced dives). It is possible, however, to derive an estimate of absolute blood flows from the data in Table 1 by using values reported in the literature for cardiac stroke volume in resting, exercising and diving ducks (Jones and Holeton, 1972; Butler *et al.* 1988; Bevan, 1990), and assuming that the heart, brain and leg muscles were the sole source of radioactivity in the respective regions of the image. In support of the above assumption, examination of lateral images confirmed that tissues lying dorsal and ventral to the brain (i.e. the scalp and tissues of the bill and pharynx) and the heart (i.e. the lungs and pectoral muscles) made only a small contribution to the total count from these regions. Tissue masses, measured in four redhead duck cadavers (body mass=0.84±0.037 kg), were as follows (mean± S.E.M.): total hindlimb muscle, 85.2±3.7 g; brain, 5.4±0.1 g; heart, 7.8±0.6 g. These data were used in calculations of mass-specific blood flow, confirming that, although the proportion of cardiac output which perfused the brain increased during forced dives, the changes in absolute blood flow were comparatively small. Conversely, hindlimb blood flows did vary in different behaviours, increasing to over twice the resting level during swimming and escape dives and decreasing to less than 30 % of the resting value during forced dives.

In conclusion, this radiological imaging method has provided data which support the hypothesis that blood flow distribution in unrestrained diving ducks with access to the water surface is the same as that during exercise without breath-hold. In addition, the emphasis can shift towards the forced dive response (i.e. reduced leg muscle perfusion) if the birds are trapped under water during an escape dive. However, the oxygen-conserving response, which is very clearly seen as preferential blood flow in the cerebral circulation during forced dives of restrained ducks, was seen in only one of four trapped escape dives. With the exception of trapped escape dives, these data confirm speculations about blood flow patterns based on measurements of heart rate, rates of oxygen consumption, size of oxygen store and patterns of diving behaviour (Eliassen, 1960; Butler, 1982; Stephenson and Jones, 1989) but there is clearly a need to investigate further the mechanisms controlling the response to being trapped under water and the apparent variability under different circumstances.

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