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REGIONAL DISTRIBUTION OF BLOOD FLOW DURING SWIMMING IN THE TUFTED DUCK (*AYTHYA FULIGULA*)

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SUMMARY

The distribution of blood flow to a number of organs and tissues of the tufted duck was determined (by the microsphere technique) before and while the birds were swimming at close to their maximum sustainable velocity (i.e. at $0{\cdot}69 \pm 0{\cdot}01\ m\ s^{-1}$).

During swimming, oxygen uptake was twice the pre-exercise value. Cardiac output increased by 70%, there was no significant change in arterial blood pressure and total systemic conductance increased by 44%. There were no significant changes in blood flow to the brain, liver, adrenal glands, spleen and respiratory muscles. Not surprisingly, there were increases in blood flow to the heart (30% increase) and to the muscles of the hindlimbs (to 3·1 times the pre-exercise value). Significant reductions in flow occurred to various parts of the gastrointestinal tract (although not to the gastrointestinal tract as a whole), to the pancreas and to the pectoralis muscles. In the case of the flight musculature as a whole, the reduction was to approximately 40% of the values in the ducks before exercise.

Thus, despite the fact that cardiac output was some three times lower than it would have been during flight, there was a clear redistribution of blood away from some visceral organs and inactive muscles during surface swimming in the tufted duck. This lends support to the suggestion that blood is selectively directed to the legs, as well as to the brain and central nervous system (CNS) and away from the visceral organs and inactive muscles during voluntary diving in these birds.

INTRODUCTION

During exercise, when perfusion of the active muscles increases, there is often a reduction in blood flow to visceral organs in a number of different species of mammals, particularly at high levels of exercise (Wade *et al.* 1956; Fixler, Atkins, Mitchell & Horwitz, 1976; Sanders, Werner & Bloor, 1976; Laughlin & Armstrong, 1982; Hohimer, Hales, Rowell & Smith, 1983; Manohar, 1986). In primates there is

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also evidence that blood flow declines to non-working skeletal muscles (Bevegard & Shepard, 1966; Hohimer *et al.* 1983), although this has not been substantiated in ponies (Manohar, 1986) and is not consistently the case in dogs (Pannier & Leusen, 1977; Musch *et al.* 1987). In dogs and ponies, only relatively small muscles, such as the temporal muscle of the head, show a decline or no increase in blood flow during exercise, indicating that few skeletal muscles are inactive during running.

On the basis of the symmorphosis hypothesis of Weibel *et al.* (1981), the oxygen delivery properties of the cardiovascular system in mammals are matched to the high oxidative demands of maximum exercise (running). Most of the skeletal muscles are involved in running, particularly in quadrupeds, so any redistribution of blood flow to these active muscles will depend mainly on vasomotor changes in the visceral organs. In most birds, however, there are two major groups of locomotory muscles which can work independently of each other.

During flight, *minimum* oxygen uptake is some 2·2 times greater than *maximum* oxygen uptake during running or swimming in birds of the same body mass (Butler, 1982*a*). Thus, because flight is the major form of locomotion in most birds, there is a large reserve capacity for oxygen transport when they are running or swimming. This would seem to make the redistribution of blood seen in mammals unnecessary.

The aim of the present study was to determine the distribution of blood throughout the body of tufted ducks while at rest and while swimming at close to their maximum sustainable velocity, using the radioactive microsphere technique.

MATERIALS AND METHODS

Six tufted ducks of either sex weighing between 0·55 and 0·70 kg were used in this study. They were raised from eggs and housed in an indoor aviary 3·3 m × 1·2 m, with a pool 3·3 m × 1·0 m × 0·4 m deep. Mixed corn and growers' pellets (Heygate & Sons Ltd) supplemented by Vionate (E. R. Squibb & Sons Ltd) were available on a dry area; in addition, mixed corn was thrown onto the pool. The birds were exposed to normal cycles of day length. A pulse-interval-modulated radiotransmitter (Butler & Woakes, 1982) was implanted under halothane anaesthesia into the abdominal cavity of each bird (for details see Stephenson, Butler & Woakes, 1986). A week later they were trained to swim on a variable-speed water channel (Armfield Engineering Ltd), the test section of which was 0·5 m square with 0·4 m depth of water. Water velocity could be varied between 0 and 1·0 m s^{-1} and was measured by a Braystoke BFM 002 current flow meter. Training lasted for at least a week, by which time the birds could hold station in the test section and swim continuously for at least 20 min at approximately 0·7 m s^{-1}. Each duck was then placed in an open-circuit respirometer on the water channel so that heart rate and oxygen uptake could be measured at rest and when swimming at approximately 0·7 m s^{-1} (for details see Woakes & Butler, 1983).

The left carotid artery and the left ventricle (*via* the right brachial artery) were then cannulated with polyethylene tubing (1·22 mm o.d., 0·96 mm i.d. and 0·96 mm o.d., 0·56 mm i.d., respectively) under halothane anaesthesia. The tip of the tubing

used to cannulate the left ventricle was plugged with a rounded blob of Araldite and a hole was cut into the side of the tubing close to the tip. The other end of the tubing was attached to a pressure transducer (Druck Ltd) so that blood pressure was continually monitored. A change in pressure pulse indicated when the catheter tip had passed into the lumen of the left ventricle. The position of the catheter in the ventricle was checked throughout the study by continually monitoring left ventricular pressure and was verified by *post mortem* examination. Body temperature was maintained by a thermostatically controlled heated blanket (Bioscience Ltd).

Each bird was allowed to recover from the anaesthetic for at least 2 h in a darkened box and then for at least another hour inside the respirometer on the water channel. When steady, low values of heart rate had been obtained, resting values of heart rate and body temperature were obtained from the implanted transmitter (Woakes & Butler, 1983) and oxygen uptake from the open circuit respirometer. Arterial blood pressure was monitored *via* the catheter in the carotid artery connected to Druck pressure transducers and recorded onto a Lectromed thermal pen recorder with rectilinear coordinates.

Regional distribution of blood flow was determined using microspheres $15 \pm 1{\cdot}5\,\mu m$ in diameter and labelled with ^{57}Co or ^{113}Sn (New England Nuclear, Stevenage). A syringe containing 0·6–0·8 ml of saline (plus 0·01 % Tween-80) containing $6–8\times10^5$ microspheres labelled with ^{57}Co was agitated vigorously with a Whirlimixer for approximately 10 min. Ten seconds before injection of this suspension into the left ventricle, blood was withdrawn from the carotid artery at a rate of $1{\cdot}63\,ml\,min^{-1}$ by a precision withdrawal pump (Braun Ltd). The suspension of microspheres was injected into the ventricle at a uniform rate and the catheter flushed with warm (41 °C) saline over a period of approximately 20 s. The withdrawal of blood from the carotid artery was terminated approximately 30 s after injection of the microspheres had ceased. Blood samples from the carotid artery at the end of this period contained no more activity than background, indicating that the withdrawal time was adequate for all of the microspheres to become lodged in the tissues (Faraci, Kilgore & Fedde, 1984). Once this procedure had been completed for the resting bird, the water channel was turned on and the animal swam at approximately $0{\cdot}7\,m\,s^{-1}$ for 20–30 min when the complete set of variables was measured again, except that this time the microspheres were labelled with ^{113}Sn. There were no significant effects of injecting the microspheres on heart rate or blood pressure.

On completion of the experiment, the birds were killed with an overdose of Sagatal (May & Baker Ltd). Various organs and tissues were carefully dissected free and, together with the reference blood samples, a known volume of well-suspended microspheres in saline and the syringe/injection assembly, were transferred to counting vials. The radioactivity of the ^{57}Co and ^{113}Sn in each of the samples was determined by an automatic gamma counter (Packard 5600 Autogamma counter, Packard Ltd). The number of counts per minute from ^{113}Sn microspheres counted in the wavelength window for ^{57}Co was corrected for, and background activity was counted in three or four empty vials. The total number of counts initially in the syringe was calculated from the counts in the known volume of well-suspended

microspheres in saline. The total number of counts injected was determined by subtracting from this value the residual counts in the syringe/injection assembly. Calculations of blood flow were as follows:

$$\text{Tissue blood flow } (\text{ml min}^{-1}) = \frac{\text{counts min}^{-1} \text{ in tissue}}{\text{counts min}^{-1} \text{ in blood sample}} \times \text{rate of withdrawal of blood sample } (\text{ml min}^{-1}),$$

$$\text{Cardiac output } (\text{ml min}^{-1}) = \frac{\text{total counts min}^{-1} \text{ injected}}{\text{counts min}^{-1} \text{ in blood sample}} \times \text{rate of withdrawal of blood sample } (\text{ml min}^{-1}).$$

Blood flows to right and left kidneys, right and left semitendinosus, right and left pectoralis, and right and left supracoracoideus muscles were not significantly different in birds before or during exercise (see Tables 2, 3), indicating that there had been adequate mixing of the microspheres in the blood upon injection into the ventricle. Samples from the lungs indicated that less than 2% of the injected microspheres reached the pulmonary vascular bed both before and during exercise (Table 2). As some of these would have been delivered directly from the left ventricle to the bronchial circulation, somewhat less than 2% of microspheres were not trapped in the peripheral circulation and thus recirculated. Therefore, the error resulting from non-entrapment of the microspheres is small (Archie *et al.* 1973). All tissue, organ (except the adrenals) and reference blood samples used in the analysis contained >400 microspheres, thus allowing valid statistical estimates of blood flows to be made (Buckberg *et al.* 1971). The number of microspheres in the adrenal glands was fewer than 400 (see Faraci, Kilgore & Fedde, 1985, working on bar-headed geese). In the three animals with the greatest numbers of microspheres in the adrenals, the mean values were 426 ± 66 at rest and 268 ± 59 during exercise. Thus, the error in calculated flow to this organ is likely to exceed ±10% (Buckberg *et al.* 1971).

As cardiac output ($\dot{V}b$) and oxygen uptake ($\dot{V}_{O_2}$) are known, the difference in arterial and venous oxygen content, or total tissue oxygen extraction, $Ca_{O_2} - C\bar{v}_{O_2}$, was calculated from the Fick equation:

$$\dot{V}_{O_2} = \dot{V}b(Ca_{O_2} - C\bar{v}_{O_2}).$$

Cardiac stroke volume was calculated by dividing cardiac output by heart rate at the time of injection of the microspheres. Conductance in the total systemic circulation or in a specific vascular bed was calculated by dividing cardiac output ($\text{ml min}^{-1}\text{kg}^{-1}$) or tissue blood flow ($\text{ml min}^{-1}\text{g}^{-1}$) by mean arterial blood pressure (kPa), calculated as diastolic pressure + 1/3 pulse pressure.

Mean values are given ±S.E. A one-way analysis of variance and paired *t*-test were used to determine any difference between any two mean values. The word 'significant' in the present report means at the 95% confidence limit ($P < 0.05$).

RESULTS

The measured variables in ducks at rest and while swimming at approximately $0.7\ \text{m s}^{-1}$, before and after insertion of the catheters, are given in Table 1. Before

Table 1. *Mean ± S.E. of oxygen consumption and cardiovascular variables in six tufted ducks before and during swimming on a water channel*

	Pre-exercise	Swimming
Before cannulation		
Velocity ($m\,s^{-1}$)	0	0·71 ± 0·01
Oxygen uptake ($ml\,min^{-1}\,kg^{-1}$)	20 ± 2	44 ± 2**
Heart rate ($beats\,min^{-1}$)	128 ± 8	224 ± 13**
After cannulation		
Velocity ($m\,s^{-1}$)	0	0·69 ± 0·01
Before injection of microspheres		
Arterial blood pressure (kPa)	21·9 ± 0·8	21·7 ± 1·1
	12·5 ± 1·9	14·3 ± 1·6
Heart rate ($beats\,min^{-1}$)	221 ± 28*	308 ± 39*,**
During injection of microspheres		
Oxygen uptake ($ml\,min^{-1}\,kg^{-1}$)	26 ± 4	53 ± 8**
Cardiac output ($ml\,min^{-1}\,kg^{-1}$)	457 ± 74	772 ± 84**
Heart rate ($beats\,min^{-1}$)	199 ± 21*	297 ± 19*,**
Cardiac stroke volume ($ml\,kg^{-1}$)	2·7 ± 0·7	2·6 ± 0·3
Arterial-venous oxygen content (vol%)	6·2 ± 1·0	7·4 ± 1·3
Total systemic conductance ($ml\,min^{-1}\,kg^{-1}\,kPa^{-1}$)	32 ± 7	46 ± 3**
After injection of microspheres		
Arterial blood pressure (kPa)	21·1 ± 1·5	20·3 ± 1·1
	12·0 ± 1·3	12·9 ± 1·2
Heart rate ($beats\,min^{-1}$)	234 ± 29*	304 ± 30*,**
Body mass (kg)	0·604 ± 0·028	

Data are given before and after cannulation of a carotid artery and the left ventricle, and before, during and after injection of microspheres into the ventricle.

*A significant difference ($P < 0·05$) between pre- and post-cannulation; **a significant difference between pre-exercise and swimming values.

insertion of the catheters, exercise caused a 2·2-fold increase in oxygen uptake and a 75% increase in heart rate. After cannulation of the blood vessels there was a significant increase in heart rate, both at rest and during exercise, compared with the values beforehand. There were, however, no significant effects on oxygen uptake.

The proportional changes in these two variables during exercise were slightly smaller in the ducks after cannulation, there being a doubling in oxygen uptake and a 50% increase in heart rate. There was no significant change in cardiac stroke volume, but oxygen extraction from the blood ($Ca_{O_2} - C\bar{v}_{O_2}$) increased by 20% and cardiac output rose by 70%. There was no significant change in arterial blood pressure during exercise, and total systemic conductance increased by 44%. Injection of the microspheres had no significant effects on heart rate or arterial blood pressure (Table 1).

Mass-specific blood flows to a number of organs and tissues before and during exercise are given in Table 2. It is interesting that the spleen was perfused at an

Table 2. *Mean ± S.E. of mass-specific blood flows to a number of different organs and tissues in the tufted duck before and while swimming at a mean velocity of 0·69 ± 0·01 m s^{-1}*

Blood flow (ml min^{-1} g^{-1})	Pre-exercise	Swimming
Brain	1·05 ± 0·13 (6)	1·05 ± 0·27 (6)
Heart	2·82 ± 0·20 (5)	3·64 ± 0·27* (5)
Lungs	0·37 ± 0·14 (6)	0·28 ± 0·12 (6)
Liver	0·53 ± 0·13 (6)	0·58 ± 0·19 (6)
Crop	0·20 ± 0·03 (5)	0·08 ± 0·01* (5)
Proventriculus	1·14 ± 0·26 (6)	0·85 ± 0·30 (6)
Gizzard	0·38 ± 0·09 (6)	0·22 ± 0·06* (6)
Duodenum	2·43 ± 0·82 (6)	1·93 ± 0·68 (6)
Intestine	0·94 ± 0·13 (6)	0·60 ± 0·08* (6)
Spleen	31·09 ± 9·71 (6)	16·70 ± 6·67 (6)
Pancreas	1·14 ± 0·14 (6)	0·71 ± 0·11* (6)
Kidney (right)	5·51 ± 1·06 (6)	3·37 ± 0·89* (6)
(left)	6·07 ± 0·90 (6)	4·08 ± 1·15 (6)
Eye (right)	0·51 ± 0·18 (5)	0·45 ± 0·13 (5)
(left)	0·42 ± 0·16 (4)	0·45 ± 0·07 (5)
Adrenal glands	2·78 ± 1·11 (3)	1·69 ± 0·24 (3)
Respiratory muscles		
intercostals	0·53 ± 0·07 (3)	0·55 ± 0·21 (3)
abdominal	0·37 ± 0·12 (6)	0·31 ± 0·09 (6)
Pectoralis muscle		
(right)	0·27 ± 0·06 (6)	0·09 ± 0·02* (6)
(left)	0·25 ± 0·05 (6)	0·11 ± 0·02* (6)
Supracoracoideus		
(right)	1·68 ± 0·43 (6)	0·67 ± 0·23 (6)
(left)	1·81 ± 0·45 (6)	0·69 ± 0·20 (6)
Total hindlimb muscle	1·07 ± 0·26 (6)	3·36 ± 0·30* (6)

The number of observations is given in parentheses and * indicates a significant difference between pre-exercise and swimming values ($P < 0·05$).

exceptionally high rate. Absolute blood flows to a number of major vascular beds before and during exercise are shown in Fig. 1. Exercise caused no significant changes in blood flow to the brain, liver, kidneys, adrenal glands, spleen, supracoracoideus and respiratory muscles. Not surprisingly, during exercise there were significant increases in blood flow to the heart (30% increase) and to the muscles of the hindlimbs (3·1 times the pre-exercise value). Significant reductions in flow occurred to various parts of the gastrointestinal tract (although not to the gastrointestinal tract as a whole), to the pancreas and to the pectoralis muscles. In the case of the flight muscles as a whole, the reduction was to approximately 40% of the values before exercise.

Further details of mass-specific blood flow to the hindlimb musculature are given in Tables 3 and 4. There were significant increases in flow to all the calf muscles and

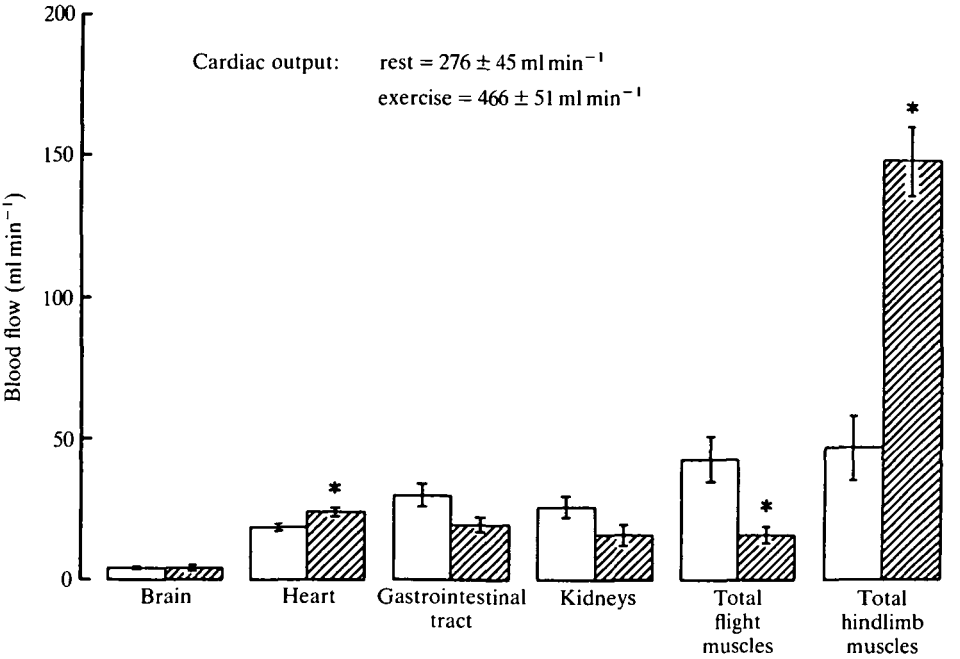

Fig. 1. Histograms showing mean (±S.E.) values of blood flow to some major vascular beds in six tufted ducks before (open bars) and while swimming at a mean velocity of 0·69 ± 0·01 m s^{-1} (hatched bars). * indicates a significant difference between pre-exercise and swimming values ($P < 0·05$).

to all but four of the thigh muscles during exercise. By far the greatest increases (to approximately seven times the values before exercise) were in the flexor perforans et perforatus digiti II and III muscles. Increases to approximately five times the values before exercise were seen in the internal femoris tibialis, the biceps femoris, the soleus and the red portion of the gastrocnemius externus muscles. For all the other muscles, blood flow increased to 1·7–4·7 times the values prior to exercise. As there was no change in arterial blood pressure during exercise, whole body and regional conductance varied directly with changes in blood flow; for example, conductance in the leg musculature increased threefold, from 0·07 ± 0·02 to 0·21 ± 0·02 ml min^{-1} g^{-1} kPa^{-1} during exercise, whereas conductance in the flight musculature decreased from 0·03 ± 0·005 to 0·01 ± 0·002 ml min^{-1} g^{-1} kPa^{-1} during exercise.

DISCUSSION

As has been found previously (Woakes & Butler, 1986), surgical procedures have a significant effect on heart rate in tufted ducks. Although the procedures were slightly more extensive in the present study (a catheter was placed into the lumen of the left ventricle), heart rates before and during swimming were not significantly different between the two studies. Oxygen uptake was slightly higher in the present study, whereas arterial blood pressure was lower in the birds in the present investigation.

Table 3. *Mean ± S.E. of blood flows to muscles and parts of muscles in the thigh of the left leg of the tufted duck before and while swimming at a mean velocity of 0·69 ± 0·01 m s^{-1}*

Blood flow (ml min^{-1} g^{-1})	Pre-exercise	Swimming
Ilio-tibialis	0·71 ± 0·22 (6)	0·78 ± 0·14 (6)
Sartorius	1·70 ± 0·53 (6)	1·59 ± 0·21 (6)
Femorotibialis externus	0·99 ± 0·29 (6)	1·96 ± 0·66 (6)
Femorotibialis medialis	0·75 ± 0·23 (6)	1·22 ± 0·25 (6)
Femorotibialis internus	0·88 ± 0·17 (6)	4·66 ± 0·88* (6)
Biceps femoris	0·65 ± 0·21 (6)	3·48 ± 0·89* (6)
Semitendinosus		
(right)	0·56 ± 0·16 (6)	2·06 ± 0·22* (6)
(left)	0·68 ± 0·19 (6)	2·12 ± 0·21* (6)
Piriformis pars caudofemoralis	1·10 ± 0·26 (6)	2·24 ± 0·31* (6)
Piriformis pars iliofemoralis	1·31 ± 0·31 (6)	2·25 ± 0·17* (6)
Semimembranosus	0·90 ± 0·32 (5)	4·03 ± 0·39* (5)
Ischiofemoralis	0·88 ± 0·24 (6)	2·64 ± 0·40* (6)
Adductor longus externus	0·91 ± 0·21 (6)	3·28 ± 0·24* (6)
Adductor longus internus	1·08 ± 0·31 (6)	3·23 ± 0·38* (6)
Ambiens	0·69 ± 0·18 (6)	2·53 ± 0·35* (6)
Iliotrochantericus posterior	1·62 ± 0·81 (5)	4·47 ± 0·93* (5)
Iliotrochantericus anterior	1·17 ± 0·37 (5)	2·61 ± 0·83* (5)
Thigh flexors	1·11 ± 0·14 (7)	2·72 ± 0·47* (7)
Thigh extensors	0·92 ± 0·08 (8)	2·79 ± 0·22* (8)

The number of observations is given in parentheses and * indicates a significant difference between pre-exercise and swimming values ($P < 0·05$).

Cardiac output before exercise was within the range determined by other workers for inactive ducks and pigeons (Butler, West & Jones, 1977; Jones *et al.* 1979; Grubb, 1982; Bech & Nomoto, 1982) and the calculated values for $Ca_{O_2}-C\bar{v}_{O_2}$, before and during exercise, were similar to those measured by Grubb (1982). The reciprocal of vascular conductance (i.e. peripheral vascular resistance), before and during exercise, was similar to that determined by Bech & Nomoto (1982), although these authors felt that their values were rather low, mainly as the result of a high value for cardiac output which was, in turn, related to a high value for oxygen uptake in the non-exercising, but instrumented, ducks. This emphasizes the observation that following surgery a number of variables may not reach true resting values. Thus, the use of the term 'rest' has been avoided in the present paper and the period of relative inactivity before the period of exercise is merely referred to as 'before exercise' or the 'pre-exercise period'.

It would appear that cardiac stroke volume does not change during flight in pigeons or during running or swimming in ducks (Butler *et al.* 1977; Bech & Nomoto, 1982; Grubb, 1982). However, in pigeons, emus and cockerels cardiac stroke volume does increase during running (Grubb, 1982; Grubb, Jorgensen &

Table 4. *Mean ± S.E. of blood flows to muscles and parts of muscles in the calf of the left leg of the tufted duck before and while swimming at a mean velocity of* $0{\cdot}69 \pm 0{\cdot}01\ m\ s^{-1}$

Blood flow ($ml\ min^{-1}\ g^{-1}$)	Pre-exercise	Swimming
Peroneals	0·69 ± 0·26 (6)	3·22 ± 0·49* (6)
Gastrocnemius externus (red)	1·68 ± 0·47 (6)	8·63 ± 1·58* (6)
Gastrocnemius externus (white)	0·88 ± 0·25 (6)	3·50 ± 0·82* (6)
Gastrocnemius medialis (red)	1·38 ± 0·32 (6)	6·13 ± 0·66* (6)
Gastrocnemius medialis (white)	1·27 ± 0·39 (6)	5·42 ± 0·70* (6)
Gastrocnemius internus (red)	1·25 ± 0·28 (6)	5·25 ± 0·69* (6)
Gastrocnemius internus (white)	0·64 ± 0·15 (6)	2·15 ± 0·47* (6)
Tibialis anterior (deep)	1·85 ± 0·57 (6)	4·92 ± 0·71* (6)
Tibialis anterior (superficial)	1·34 ± 0·48 (6)	4·71 ± 0·78* (6)
Extensor digiti longus	1·59 ± 0·47 (6)	3·95 ± 0·65* (6)
Flexor digiti longus	1·11 ± 0·39 (6)	3·69 ± 0·50* (6)
Flexor perforans et perforatus digiti II	0·94 ± 0·31 (6)	6·36 ± 0·87* (6)
Flexor perforans et perforatus digiti III	0·94 ± 0·28 (6)	6·62 ± 0·45* (6)
Flexor perforatus digiti IV	1·15 ± 0·37 (5)	4·35 ± 0·87* (5)
Soleus	0·78 ± 0·20 (6)	4·31 ± 0·70* (6)
Toe flexors	1·49 ± 0·39 (5)	4·18 ± 0·72* (5)
Calf flexors	1·26 ± 0·11 (7)	5·11 ± 0·43* (7)
Calf extensors	1·13 ± 0·12 (9)	4·73 ± 0·66* (9)

The number of observations is given in parentheses and * indicates a significant difference between pre-exercise and swimming values ($P < 0{\cdot}05$).

Conner, 1983; Barnas, Gleeson & Rautenberg, 1985). As predicted by Woakes & Butler (1986), there was an increase in $Ca_{O_2} - C\bar{v}_{O_2}$ during swimming in the tufted ducks, despite the fact that heart rate was well below its maximum value.

As birds have a greater cardiac output for a given oxygen consumption than mammals of similar size (Grubb, 1983), it is not surprising to find that mass-specific blood flow to most tissues and organs of the tufted duck before exercise is greater than that in a number of mammals (Pannier & Leusen, 1977; Armstrong & Laughlin, 1985; Armstrong, Delp, Goljan & Laughlin, 1987). Notable exceptions to this difference in perfusion between birds and mammals were the kidneys. These organs receive the highest mass-specific flow in mammals, similar in value to that in the tufted duck. However, the organ with the highest mass-specific flow in the tufted duck and in other birds (Faraci *et al.* 1985) is the spleen. The significance of this is unclear.

Within the gastrocnemius externus muscle of the tufted duck, the red portion consists of a greater percentage of fast oxidative glycolytic (FOG) fibres than the white portion (Turner & Butler, 1988), which relates to the higher blood flows to the red portion both before and during exercise. Although the differences are not nearly as great as in the rat (Armstrong & Laughlin, 1983; Laughlin, Mohrman & Armstrong, 1984), they are similar to those in pigs (Armstrong *et al.* 1987).

Despite the substantial increase in lung ventilation during swimming in ducks (Woakes & Butler, 1986), there was no change in blood flow to either the intercostal or the abdominal respiratory muscles. A possible explanation for this lies in Woakes & Butler's finding of a fixed 6:1 relationship between leg beat frequency and respiratory frequency when tufted ducks are swimming at 0·7–0·8 $m s^{-1}$. This relationship may, in some way, substantially reduce the energetic cost of lung ventilation, at least as far as the respiratory muscles themselves are concerned. It must be pointed out, however, that in ponies, where a fixed 1:1 relationship exists between limb movement and ventilation during cantering and galloping (Bramble & Carrier, 1983), there is, nonetheless, a large increase in blood flow to the diaphragm (Parks & Manohar, 1983).

Perhaps the most interesting aspect of the present results is the *reduction* in blood flow, not only to some visceral organs but also to the pectoralis muscles, during swimming. During flight, cardiac output in a pigeon can reach 2·41 $kg^{-1} min^{-1}$ (Butler *et al.* 1977), which is some three times that recorded in the tufted duck, swimming at 0·7 $m s^{-1}$. There would seem, therefore, to be no 'pressure' on the cardiovascular system in volant birds when running or swimming to divert blood away from the visceral organs and inactive muscles. In fact, in one study on exercising dogs, such a diversion of blood from the visceral vascular beds was only seen after surgically induced heart block had prevented the normal increase in heart rate (Vatner *et al.* 1971). Nonetheless, such a redistribution did occur in the tufted duck when swimming close to its maximum sustainable velocity. The functional significance of this may be that it is energetically less costly to redistribute blood flow than to increase cardiac output.

Before swimming, 16·2% of cardiac output went to the legs, 9·7% to the gastrointestinal tract, 9·0% to the kidneys and 14·9% to the flight muscles. During swimming, when cardiac output had increased by 70%, these proportions changed to 31·8%, 3·9%, 3·6% and 3·5%, respectively. The proportion of cardiac output going to the legs in swimming tufted ducks compares with approximately 87% of cardiac output going to working skeletal muscle in maximally exercising pigs and other mammals (Armstrong *et al.* 1987). The observation that such a large redistribution of blood flow does occur in the tufted duck when swimming close to its maximum sustainable velocity at the surface lends support to the suggestion that blood is selectively directed towards the legs, as well as to the brain and CNS, and away from the viscera and inactive muscles during voluntary diving in these birds (Butler, 1982*b*).

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