

EFFECT OF TRAINING ON MAXIMAL OXYGEN UPTAKE AND AEROBIC CAPACITY OF LOCOMOTORY MUSCLES IN TUFTED DUCKS, *AYTHYA FULIGULA*

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SUMMARY

1. The effects of artificial swim training on maximal oxygen consumption and heart rate, as well as on the capillarity and oxidative capacity of locomotory muscles, have been studied in the tufted duck, *Aythya fuligula*.

2. The artificial training programme resulted in a 27% increase in maximal oxygen consumption, mainly as a result of an increase in muscle capillarity (20% increase in capillary/fibre ratio). In addition, activity of an oxidative enzyme, citrate synthase, increased (by 42%) and there was a significant transformation of fibre types in the lateral gastrocnemius muscle.

3. Altering the duration and nature of the training stimulus, for example flying and diving, can bring about different degrees of muscular adaptation, particularly in oxidative capacity.

INTRODUCTION

Only a few studies on birds have involved exercise training for prolonged periods (Butler, West & Jones, 1977; Brackenbury & El-Sayed, 1985; Rothe, Biesel & Nachtigall, 1987). Even then, training was only employed so that reliable/reproducible measurements of physiological variables could be obtained during exercise. The effect of training, *per se*, in birds has not yet been investigated in detail. Anecdotal reports describe exercise training as increasing both maximal oxygen consumption (Brackenbury & El-Sayed, 1985) and the activity of an aerobic enzyme, fumerase, in muscle (Matsuda, Zernicke, Vailas, Pedrini, Pedrini-Mille & Maynard, 1986), suggesting that adaptations do occur.

It is known that endurance training in mammals and man leads to an increase in maximal oxygen consumption (Holloszy & Booth, 1976). Furthermore, by employing an appropriate training regime, the overall respiratory capacity of muscle can also increase. This is a result of increases in the capacity to oxidize carbohydrate and lipid, accompanied by a parallel rise in the capacity to generate ATP via oxidative phosphorylation (Baldwin, Klinkerfuss, Terjung, Mole & Holloszy, 1972). There are increases in the activities of enzymes involved in the β -oxidation of long-chain free

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fatty acids and in the tricarboxylic acid cycle and an increase in components of the mitochondrial respiratory chain (Holloszy & Booth, 1976). The increases in enzyme protein concentration (activity) appear to be linked to an increase in the mitochondrial content of muscle fibres (Hoppeler, 1986). However, the increases in the respiratory capacity of muscle after training are not always well correlated with the smaller increases in maximal oxygen consumption (Davies, Packer & Brooks, 1981).

After endurance training there is often an increase in muscular capillarity (Andersen & Henriksson, 1977; Adolfsson, Ljungqvist, Tornling & Unge, 1981) which presumably increases the surface area for diffusion of oxygen from blood to muscle cell and also maintains a long mean transit time for blood through the muscle (Saltin, 1985). Capillary growth seems to be directed to more frequently recruited fibres and thus is dependent on the intensity of exercise training (Hudlicka, 1982).

If endurance training is sufficiently intense and long, there can be some degree of fibre-type transformation. Studies have shown such transformations from fast glycolytic (FG) to fast oxidative glycolytic (FOG) fibres, from FOG to fast-slow twitch intermediate fibres (sometimes denoted as IIC) and from intermediate and FOG fibres to slow oxidative (SO) fibres (Ingjer, 1979; Green, Klug, Reichmann, Seedorf, Wieher & Pette, 1984; Howald, Hoppeler, Claasen, Mathieu & Weibel, 1985).

Species of birds that are more active in their lifestyle tend to have muscles with higher oxidative capacities than more sedentary species (Pages & Planas, 1983; Palacios, Palomeque, Riera, Viscor & Planas, 1984; Thomas, 1985). Although there may be a significant degree of heredity involved in the development of muscular endowment in these species (Nimmo, Wilson & Snow, 1985), there may also be a training effect imposed on the muscles by life-long exercise. The search for a causal relationship between life-long exercise training and the genetic coding for pre-determined phenotypic endowment is currently an expanding area of study (Pette, 1986).

The possibility therefore exists for marked differences in the muscular and cardiorespiratory systems to occur in birds that have undertaken different forms and intensities of exercise training. The tufted duck is a species that can fly, swim, dive and run, so it should be possible to ascertain the effect of training on this species during different types of locomotory activity. The aim of this study was to describe the adaptations that the tufted duck shows to different types and durations of artificial and natural training.

METHODS

Animals and training

Juvenile tufted ducks, *Aythya fuligula*, were randomly assigned to one of two groups. The first group of six ducks was kept on a deep diving pool (10 × 4.5 × 1.9 m; 2.8 m deep) within the confines of an outdoor compound (13 × 6.5 × 3.0 m high). These birds took part in natural activity (flying, diving, swimming, etc.) for at least 6 months. The majority of the pool was covered with plastic mesh and in order to obtain food (mixed corn), 5 days a week, they had to dive to between 1.9 and 2.8 m over distances up to 12 m (see Stephenson, Butler & Woakes, 1986, for details of pool design).

Progressive training meant that they were competent at diving for longer than 40 s, which is close to the calculated maximum duration for this species (Keijer & Butler, 1982). For 2 days a week the corn diet was supplemented with growers' pellets, available on a dry area adjacent to the pool. These ducks are designated as naturally trained (NT).

The second group, containing twelve tufted ducks, was kept in an indoor aviary as described previously (Turner & Butler, 1988). Six of these ducks underwent only little exercise due to the confines of the indoor aviary and pool and are designated as untrained (UT), whereas the other six undertook a progressive programme of artificial endurance training. During an initial period of 2 weeks the ducks swam on a water flume at a velocity of 0.65 m s^{-1} , 4 days a week. The duration increased from 45 to 90 min by the end of the second week. During weeks 3–6 the swimming velocity was increased to 0.70 m s^{-1} , with the duration increasing from 90 to 180 min. The frequency of exercise bouts was maintained at 4 days a week. During weeks 7–9 ducks could swim at 0.72 m s^{-1} for 180 min, 5 days a week comfortably. At this final velocity (0.72 m s^{-1}) oxygen consumption was approximately 85% of maximum oxygen consumption in untrained ducks. These ducks are designated as artificially trained (AT).

Physiological measurements

In order that reliable and reproducible physiological measurements were obtained, the following protocol was implemented so that untrained (UT) and artificially trained (AT) ducks were subjected to similar conditioning, etc. (with the exception of the training itself). Both UT and AT ducks were familiarized with swimming on a variable-speed water channel (Armfield Engineering Limited). Each duck was restricted to an area of 0.4 by 0.2 m within a Perspex respirometer box (Woakes & Butler, 1983) and swam for 15–20 min at speeds of 0.25, 0.35, 0.45, 0.55 and 0.65 m s^{-1} . The order of the swimming bouts was random. Once familiarization was complete each duck could swim steadily at any of the allotted velocities for at least 15 min. The ducks to be trained were then subjected to the progressive endurance training programme described above. Oxygen consumption (\dot{V}_{O_2} ; STPD and measured by open-circuit respirometry; Turner, 1987) and heart rate (measured via an implanted radiotransmitter; see Stephenson *et al.* (1986) for the details of surgery) were monitored throughout the last 10 min of each swimming bout. Each session ended with a 15–20 min swimming bout at the maximum sustainable swimming speed (U_{max}). Resting measurements were taken before and after each swimming session with the flume motor off and with it on. The oxygen pulse ($\mu\text{l O}_2 \text{ beat}^{-1} \text{ kg}^{-1}$) was calculated as the ratio of oxygen consumption and heart rate. Water temperature was routinely measured and was $19 \pm 1 \text{ }^\circ\text{C}$ for the untrained ducks and $21 \pm 1 \text{ }^\circ\text{C}$ for the artificially trained ducks, there being no significant difference between the two values.

Anatomical studies

The muscles studied in this study were lateral gastrocnemius (a calf muscle) and semitendinosus (a thigh muscle), both of which receive representative increases in blood flow during swimming (Butler, Turner, Al-Wassia & Bevan, 1988), the pectoralis muscle (the major flight muscle) and the heart. Muscle samples from the three locomotory muscles were processed for fibre typing and capillarity from UT and AT ducks and processed, along with heart samples, for activities of the enzymes citrate synthase (CS), 3-hydroxyacyl-CoA-dehydrogenase (HAD) and lactate dehydrogenase (LDH) and myoglobin content at $25 \text{ }^\circ\text{C}$ as described previously (Turner & Butler, 1988). Additionally, the locomotory and heart muscles from NT ducks were analysed for enzyme activities and myoglobin content.

Statistics

Mean values are given \pm s.e. of the mean. The number of observations is represented by n . Statistical and regression analyses were performed using a BBC microcomputer and a software package (Unistat). Significant differences between mean values from different groups of ducks were determined using a one-way analysis of variance and Student's t tests for samples with unknown variances. In physiological experiments, where appropriate, a multiple paired comparisons statistical test was used (Wallenstein, Zucker & Fleiss, 1980). Results were considered significant at the 95% ($P < 0.05$) confidence level. A preliminary report of this study has been published (Butler & Turner, 1988).

RESULTS

Physiological responses to swimming in untrained ducks

There were no significant differences between oxygen consumption or heart rate measured with the flume motor switched off or with it switched on (Table 1). Comparison of variables measured during swimming will be, therefore, to values obtained when the flume motor was off. Mean oxygen consumption of six swimming

TABLE 1. Mean values (\pm S.E.M.) of variables measured in six untrained (UT) and six artificially trained (AT) tufted ducks at rest and whilst swimming on a water channel at maximal swimming velocities (U_{\max}). * Significant difference between UT and AT ducks ($P < 0.05$)

	UT	AT
Maximal swimming velocity (m s^{-1})	0.75 ± 0.01	$0.80 \pm 0.01^*$
Oxygen consumption at STPD ($\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$)		
Rest (motor off)	17.0 ± 1.3	16.7 ± 1.3
Rest (motor on)	17.9 ± 2.4	18.2 ± 0.8
At U_{\max}	48.6 ± 3.0	$61.9 \pm 2.6^*$
Heart rate (beats min^{-1})		
Rest (motor off)	115 ± 3	$97 \pm 5^*$
Rest (motor on)	120 ± 3	$103 \pm 5^*$
At U_{\max}	266 ± 21	263 ± 8
Oxygen pulse ($\mu\text{l O}_2 \text{ beat}^{-1} \text{ kg}^{-1}$)		
Rest	148 ± 10	174 ± 12
At U_{\max}	185 ± 8	$241 \pm 10^*$
Body mass (g)	638 ± 27	678 ± 25
Water temperature ($^{\circ}\text{C}$)	19 ± 1	21 ± 1

untrained ducks was first significantly higher than resting values at a speed of 0.55 m s^{-1} , at which point oxygen consumption was 81% higher than resting values (Fig. 1). At faster swimming speeds oxygen consumption increased by larger increments such that at a maximum sustainable swimming speed (U_{\max}) of $0.75 \pm 0.01 \text{ m s}^{-1}$, oxygen consumption ($\dot{V}_{\text{O}_2, \max}$) was $48.6 \pm 3.0 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$. This represents an aerobic capacity ($\dot{V}_{\text{O}_2, \max} / \dot{V}_{\text{O}_2, \text{rest}}$) of 2.92 ± 0.24 . Aerobic scope ($\dot{V}_{\text{O}_2, \max} - \dot{V}_{\text{O}_2, \text{rest}}$) was $31.2 \pm 3.2 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$. Heart rate increased in a similar fashion to oxygen consumption, first becoming significantly higher than resting at a swimming speed of 0.45 m s^{-1} . At U_{\max} , heart rate showed a 2.3-fold increase above resting. The oxygen pulse at U_{\max} was significantly higher than at rest (Table 1).

Effect of training on the physiological responses to exercise

At rest. Although oxygen consumption, at rest, was not significantly different between untrained and artificially trained ducks, resting heart rate was significantly lower in the artificially trained birds (Table 1). As a consequence, the oxygen pulse in artificially trained ducks was slightly, although not significantly, higher.

Submaximal exercise. Oxygen consumption was not significantly different between untrained and artificially trained ducks at any submaximal swimming speed, up to and including 0.75 m s^{-1} . Heart rate was significantly lower in artificially trained ducks at all submaximal swimming speeds between 0.35 and 0.75 m s^{-1} (Fig. 1).

At maximal exercise. The artificially trained ducks could swim for 20 min at a

significantly higher ($+6.7\%$) maximal swimming speed of $0.8 \pm 0.01 \text{ m s}^{-1}$ and had a significantly higher ($+27\%$) oxygen consumption at U_{max} than untrained ducks (Table 1). They also had significantly greater aerobic scope, of $45.5 \pm 3.0 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ and aerobic capacity, of 3.80 ± 0.24 ($+46$ and $+30\%$, respectively).

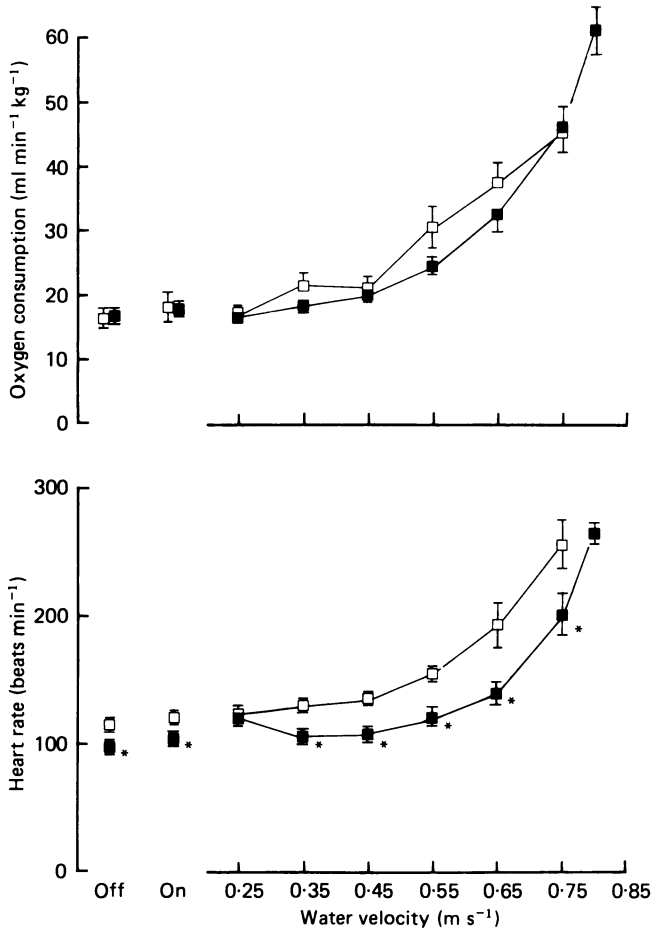


Fig. 1. Diagrams showing oxygen consumption ($\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) and heart rate (beats min^{-1}) in tufted ducks at rest with the flume motor off (Off) or on (On) and whilst they swam at a number of different velocities (m s^{-1}). Values are means (\pm s.e.m.) from six untrained (\square) and six artificially trained (\blacksquare) ducks. The asterisks represent a significant difference ($P < 0.05$) between values at the same velocity.

Heart rate at U_{max} was not significantly different between untrained and artificially trained ducks. As a consequence, the oxygen pulse at U_{max} was significantly greater ($+30\%$) in artificially trained ducks.

Anatomical studies. Ducks that were kept inside weighed significantly less than those kept outside ($638 \pm 27 \text{ g}$, UT ducks; $678 \pm 29 \text{ g}$, AT ducks; $740 \pm 24 \text{ g}$, NT ducks). However, the relative proportions of body mass made up by the lateral

TABLE 2. Mean values (\pm S.E.M.) for the morphometric fibre composition and capillarity of the red and white portions of the lateral gastrocnemius, semitendinosus and pectoralis muscles of six untrained (UT) and six artificially trained (AT) tufted ducks. * Significant difference between UT and AT ducks ($P < 0.05$)

	Red lateral gastrocnemius		White lateral gastrocnemius		Semitendinosus		Pectoralis	
	UT	AT	UT	AT	UT	AT	UT	AT
Muscle mass (g)	0.4 \pm 0.04	0.4 \pm 0.03	1.4 \pm 0.10	1.5 \pm 0.04	2.5 \pm 0.14	2.5 \pm 0.06	47.4 \pm 2.00	55.3 \pm 3.2*
Fibre type (%)								
SO	14.8 \pm 0.6	17.5 \pm 1.1*	—	—	—	—	—	—
FOG	85.2 \pm 0.6	82.5 \pm 1.1*	45.7 \pm 4.5	54.1 \pm 1.5*	51.3 \pm 3.3	51.3 \pm 1.6	87.9 \pm 2.3	89.2 \pm 0.8
FG	—	—	54.3 \pm 4.5	45.9 \pm 1.5*	48.7 \pm 3.3	48.7 \pm 1.6	12.1 \pm 2.3	10.8 \pm 0.8
Fibre area (μm^2)								
SO	962 \pm 86	1024 \pm 108	—	—	—	—	—	—
FOG	1691 \pm 151	1432 \pm 144	1320 \pm 22.8	1257 \pm 113	1253 \pm 189	1320 \pm 75	389 \pm 48	479 \pm 37*
FG	—	—	2382 \pm 359	2316 \pm 135	2405 \pm 221	2670 \pm 198	1141 \pm 123	1537 \pm 140*
Number of capillaries around a fibre								
SO	4.53 \pm 0.13	5.00 \pm 0.17*	—	—	—	—	—	—
FOG	4.83 \pm 0.14	5.30 \pm 0.10*	5.03 \pm 0.15	5.01 \pm 0.14	4.50 \pm 0.10	5.03 \pm 0.12*	4.80 \pm 0.20	5.30 \pm 0.20
FG	—	—	5.05 \pm 0.19	5.64 \pm 0.17*	5.20 \pm 0.21	5.71 \pm 0.07*	5.50 \pm 0.40	5.80 \pm 0.30
Capillary density (mm^{-2})	1313 \pm 211	1427 \pm 96	895 \pm 111	1368 \pm 95*	1106 \pm 84	1284 \pm 109	3361 \pm 399	3284 \pm 307
Capillary/fibre ratio	1.83 \pm 0.08	2.19 \pm 0.06*	1.66 \pm 0.03	1.91 \pm 0.02*	1.46 \pm 0.09	1.84 \pm 0.06*	2.20 \pm 0.11	2.41 \pm 0.18

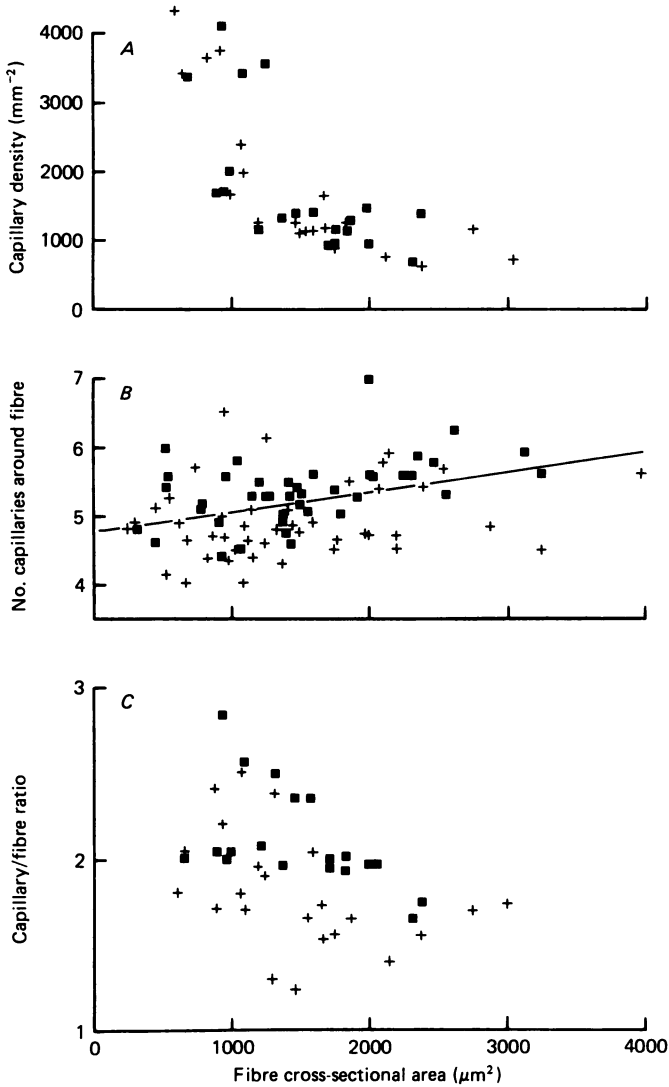


Fig. 2. The relationship between fibre cross-sectional area and capillary density (A), number of capillaries around a fibre (B) and capillary/fibre ratio (C) in the lateral gastrocnemius, semitendinosus and pectoralis muscles of six untrained ducks (+) and six artificially trained ducks (■). The regression equation describing the regression line in B is: $Y = 4.76 + 2.50 \times 10^{-4}X$ ($r = 0.33$; $P < 0.05$) where X is the fibre cross-sectional area (μm^2) and Y is the number of capillaries per fibre.

gastrocnemius, semitendinosus or heart muscles were not significantly different in any group. The muscle mass of the flight muscles (pectoralis and supracoracoideus muscles), as a proportion of body mass, was significantly higher in AT ducks, although this did not result in a significantly higher ratio of total flight muscle mass to leg muscle mass (2.63 ± 0.16 , UT ducks; 2.80 ± 0.10 , AT ducks; 2.72 ± 0.19 , NT ducks).

Fibre morphometry. Lateral gastrocnemius was the only muscle sampled where there was a different distribution of fibre types in artificially trained (AT) ducks compared to untrained individuals. As a consequence of higher percentages of SO (in the red portion of lateral gastrocnemius) and FOG fibres (in the white portion of gastrocnemius; Table 2), the overall percentage of oxidative fibres (SO + FOG) in the lateral gastrocnemius muscle as a whole was higher in AT ducks. However, in the semitendinosus muscle there was no significant difference in fibre type distribution

TABLE 3. Mean values (\pm S.E.M.) for the activities of various enzymes and myoglobin content of the lateral gastrocnemius, semitendinosus, pectoralis and heart muscles from four to six untrained (UT), six artificially (swim) trained (AT) and six naturally trained (NT) tufted ducks. Enzyme activities are expressed as $\mu\text{mol min}^{-1} \text{g}^{-1}$ fresh wet weight of muscle. *, †, ‡ significant differences: UT *vs.* AT; UT *vs.* NT; AT *vs.* NT respectively ($P < 0.05$)

	Gastrocnemius	Semitendinosus	Pectoralis	Heart
Citrate synthase				
UT	30.8 \pm 6.3	23.8 \pm 4.5	86.5 \pm 17.0	108.0 \pm 6.8
AT	45.1 \pm 2.3*	30.2 \pm 1.6	84.2 \pm 7.5	95.6 \pm 7.0
NT	94.8 \pm 3.3†‡	65.5 \pm 2.2†‡	150.8 \pm 6.7†‡	128.1 \pm 4.4†‡
3-Hydroxyacyl-CoA-dehydrogenase				
UT	9.0 \pm 1.0	8.6 \pm 1.7	19.6 \pm 3.7	23.1 \pm 4.2
AT	9.1 \pm 1.1	6.8 \pm 0.7	17.4 \pm 3.0	20.3 \pm 2.9
NT	16.6 \pm 1.2†‡	11.3 \pm 0.9†	29.5 \pm 3.3	26.8 \pm 3.1
Lactate dehydrogenase				
UT	488 \pm 68	505 \pm 54	627 \pm 50	334 \pm 31
AT	475 \pm 32	510 \pm 22	690 \pm 34	373 \pm 29
NT	415 \pm 10	491 \pm 18	563 \pm 8‡	394 \pm 18
Myoglobin content (mg g ⁻¹)				
UT	7.13 \pm 0.35	4.83 \pm 0.51	4.74 \pm 0.59	7.01 \pm 0.69
AT	6.57 \pm 0.58	5.16 \pm 0.70	5.12 \pm 0.50	6.28 \pm 0.12
NT	9.81 \pm 0.30†‡	7.41 \pm 0.30†‡	7.35 \pm 0.80†‡	6.75 \pm 0.51

or fibre cross-sectional areas between UT and AT ducks (Table 2). The significantly larger fibre cross-sectional areas of FOG and FG fibres in the pectoralis muscle of AT ducks contributed to the larger pectoralis muscle mass in AT ducks (Table 2).

Capillarity. The number of capillaries around SO fibres was significantly higher in the lateral gastrocnemius muscle of the AT ducks (Table 2). There were significantly more capillaries around FOG fibres in the red part of the lateral gastrocnemius muscle and in the semitendinosus muscle of AT ducks, but not around FOG fibres in the white part of the lateral gastrocnemius or pectoralis muscles. There were significantly more capillaries around FG fibres in the lateral gastrocnemius and semitendinosus muscles, but not in the pectoralis muscle of AT ducks.

The capillary density was only significantly greater in AT ducks in the white part of the lateral gastrocnemius muscle. Both capillary density and the number of capillaries around a fibre were significantly dependent on fibre cross-sectional area, but the capillary/fibre ratio was not (Fig. 2). Thus, a significantly greater capillarity (greater capillary/fibre ratio) was present in the white lateral gastrocnemius (20%), red lateral gastrocnemius (15%) and semitendinosus muscles (26%), but not in the pectoralis muscle of AT ducks (Table 2).

Enzyme activities and myoglobin content. The activity of citrate synthase (CS) in the lateral gastrocnemius of AT ducks was significantly higher (+42%) than that in the same muscle of UT ducks. However, the activities of 3-hydroxyacyl-CoA-dehydrogenase (HAD) and lactate dehydrogenase (LDH) in the lateral gastrocnemius muscle of AT ducks were not significantly different from those in UT ducks. There was no significant difference in any enzyme activity between the semitendinosus, pectoralis or heart muscles of AT and UT ducks. Myoglobin content was not significantly different in any muscle of UT and AT ducks (Table 3).

Citrate synthase activity was significantly higher in all four muscles sampled in NT tufted ducks than in the other two groups. HAD activity was significantly higher in the lateral gastrocnemius and pectoralis muscles of NT ducks compared to UT ducks. LDH activity of the pectoralis muscle in NT ducks was significantly lower than that in the pectoralis muscle of AT ducks. Myoglobin content was significantly higher in all muscles, except the heart, in NT ducks (Table 3).

DISCUSSION

Changes in oxygen consumption and extraction induced by swim training

The training regime employed resulted in a greater maximal oxygen consumption (27%) in AT ducks, but as maximal heart rate was unchanged, the increase in maximal oxygen consumption must have been the result of either an increase in maximal cardiac stroke volume and/or an increase in tissue oxygen extraction.

Artificially trained ducks in this study had heart masses that were not significantly heavier than those of untrained ducks (5.8 ± 0.5 g, UT; 6.5 ± 0.4 g, AT). As an increase in cardiac stroke volume is usually associated with a hypertrophy of cardiac muscle fibres (and hence an increase in mass; Blomqvist & Saltin, 1983), it seems unlikely that there has been any substantial change in maximal cardiac stroke volume in the AT ducks. Endurance training has been shown to cause an increase in heart mass in some species, but is by no means a common finding (Blomqvist & Saltin, 1983). As the hearts of birds are capable of working at much higher levels during flight than during swimming (Butler & Woakes, 1979), they are already very well adapted for producing higher cardiac outputs than will ever be needed during swimming (Butler *et al.* 1988). Therefore, it is not surprising to see no significant adaptation of the heart after artificial swim training. Similarly, the heart already has an extremely high oxidative capacity and the artificial training regime appeared to be no stimulus for an increase in oxidative capacity. It is concluded that the greater maximal oxygen consumption results from a greater tissue oxygen extraction.

The greater maximal oxygen consumption in AT ducks is accompanied by a larger capillarity. There is a significantly greater average capillary/fibre ratio in the lateral gastrocnemius (both red and white portions) and semitendinosus ($20 \pm 3\%$) muscles and, although not significant, a greater average ($26 \pm 11\%$) capillary density in the leg muscles studied. If the capillary/fibre ratio is taken to represent true capillary growth in a muscle (Hudlicka, 1985), then the majority of the increase in maximal oxygen consumption can be accounted for by an increase in capillarity, which presumably allows a larger extraction of oxygen from the blood by the muscle fibres. A close relationship between increases in maximal oxygen consumption and

capillarity after training has been found in a number of studies (Andersen & Henriksson, 1977; Ingjer, 1979). In summary, the increase in maximal oxygen consumption is due mainly to peripheral (capillarity) and not central (myocardial size and biochemical) adaptations.

The stimulus for capillary growth after training is not known for certain, but there are two main factors that have been considered. The bulk flow of blood or terminal arteriolar blood pressure may in some way stimulate a proliferation of endothelial cell growth. Alternatively, chemical signals such as hormones, local hypoxia or release of local metabolites may stimulate capillary branching and growth (Hudlicka, 1985). Presumably a slightly higher cardiac stroke volume, resulting from the small insignificantly greater heart mass and substantially larger muscle capillarity in artificially trained ducks, are sufficient to allow the lowering of heart rate during submaximal exercise while maintaining oxygen delivery to the active muscles.

Changes in muscle fibre contractile and metabolic profiles after artificial training

The lateral gastrocnemius muscle was the only muscle to show a different distribution of muscle fibres in artificially trained ducks (AT). There was a shift in the proportion of fibre types from FG to FOG to SO. This is the same trend as that in many other studies which document a fibre transformation following exercise training (Ingjer, 1979; Green *et al.* 1984; Howald *et al.* 1985) and electrostimulation of muscle (Pette & Vrbová, 1985). When the transformations are assessed in terms of the whole lateral gastrocnemius muscle, the ratio of oxidative (SO + FOG) to glycolytic (FG only) fibre masses was greater in AT ducks. Accompanying the relative increase in oxidative fibre mass in the lateral gastrocnemius muscle was a significant increase in the activity of the oxidative enzyme, citrate synthase. It is not known in the present study whether the increase in citrate synthase activity was equal in all types of fibre, but presumably the activity will only increase in those fibres that have been active at the intensity of the exercise used during training (Hickson, 1981). As there was a greater number of capillaries around all three types of fibre in the lateral gastrocnemius muscle after artificial training, indicating use of all three fibre types, it is reasonable to expect that citrate synthase activity increased in all three fibre types as well.

In the semitendinosus muscle, where there was a significant increase in the capillarity of the muscle and of each muscle fibre, there was not a significant increase in citrate synthase activity nor a significant transformation of muscle fibres. This may indicate a dissociation of circulatory and muscular adaptation in this muscle. Semitendinosus may not be active to the same degree as lateral gastrocnemius during swimming as it receives a lower mass specific blood flow during swimming (Butler *et al.* 1988). The rate of adaptation may be at a lower level than that of lateral gastrocnemius. It has been shown that capillarity generally increases before changes in muscle fibre metabolic and contractile profiles during electrostimulation (Hudlicka, Dodd, Renkin & Gray, 1982). In this muscle, it is possible that the stimulus threshold for an increase in capillarity has been reached, but that for muscle fibre adaptation has not.

Changes in muscle metabolic profile after natural training

Most birds can use two different muscle masses during different modes of locomotion. In this study, ducks have been either trained to use leg muscles only (artificially trained by swimming/no flying), leg and flight muscles (naturally trained by diving/flying) or neither muscle mass (no swimming/no diving/no flying). It is therefore possible to compare a number of different modes of training.

Influence of flight activity and captivity on the pectoralis muscle. The flight performed by the ducks in the outdoor aviary resulted in very high levels of aerobic enzyme activities. Indeed, the activities of CS and HAD in the pectoralis muscle were as high or higher than those in the heart. This has been found in other active flying birds (Suarez, Brown & Hochachka, 1986). Captivity, which impaired flight exercise, resulted in a significant reduction in the aerobic capacity of the pectoralis muscle (CS and HAD activities lower) and also in myoglobin content. The reduction of oxidative capacity has been found in captive individuals of other avian species (Pages & Planas, 1983; Palacios *et al.* 1984). Flight is a particularly intensive form of exercise and must tax the cardiovascular system more than swimming or diving. Consequently, there was also a higher aerobic capacity of the heart (CS activity higher) in active flyers.

Influence of natural and artificial training on leg muscles. Long-term natural training (for at least 6 months) included long-distance diving for food. This mode of exercise is as intense as swimming at maximal velocity at the surface (Woakes & Butler, 1983), and was a much greater stimulus for metabolic profile adaptation in the muscles than medium-term artificial swim training. There were significantly greater CS and HAD activities in both of the leg muscles that were studied after natural training compared with those after artificial training. The intensity, duration and frequency of training are all important in determining the extent of adaptation of metabolic profile in muscle (Hickson, 1981; Harms & Hickson, 1983). The overall duration of natural training was longer than that of the artificial training. The individual bouts of diving may also have been different in duration from those of swimming. Bouts of artificial training reached a maximum duration of 3 h per day (see Methods section), but in comparison under natural conditions tufted ducks have been observed to spend between 4.8 and 5.2 h per day diving (Pedroli, 1982). However, the intensity of exercise during diving and swimming (at the training velocity) are similar (Woakes & Butler, 1983). Although the electrical activity of all the muscles involved in diving or swimming in the tufted duck has not been determined, leg beat frequencies during swimming at 0.6–0.7 m s⁻¹ and during diving are similar (Butler & Woakes, 1982) so there would appear to be no great differences in the overall intensity of muscle activity between diving or swimming. In summary, the major contributor to the differences in aerobic enzyme activities between diving and non-diving groups of tufted ducks appears to be the duration of the training and not its intensity.

There was a higher myoglobin content of leg muscles in naturally trained ducks than in the other two groups. The duration of training in naturally trained ducks may have been long enough to stimulate myoglobin synthesis or the myoglobin content of the muscles studied may be the result of other influences, such as the need

to increase oxygen stores for prolonged dives (R. Stephenson, D. L. Turner, P. J. Butler, in preparation).

Some avian species that migrate are known to undergo marked adaptations in muscle aerobic capacity and fuel utilization (Marsh, 1981). However, there are a number of differences between the adaptations to training and preparation for migration. For example, endurance training increases the activity of citrate synthase, but this does not occur during pre-migratory preparation (Marsh, 1981). Care must be taken, therefore, when studying adaptations to training in captive birds, not to extrapolate to seasonal adaptations in the muscles of wild populations. It does appear from the present study, however, that prolonged periods of natural inactivity, e.g. as might occur during incubation and moulting, would most likely lead to a reduction in the aerobic capacity of all locomotory muscles and that some 'training' would then be necessary prior to any long migratory journey.

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