Physiology of Work
Conflicting Requirements of Exercise and Heat Stress for Blood Flow Distribution in Domestic Animals

A. W. Bell* and J. R. S. Hales**

The combined effects of exercise and heat stress on the human circulatory system have recently been reviewed (Brengelmann 1983; NadeI 1983; Rowell 1983). The essential physiological problems are not only the fact that the cardiovascular system must serve thermoregulatory requirements while maintaining its own integrity, but there is a 'conflict of interest' created by major increases in requirements for blood flow in both skeletal muscle and skin (Rowell 1977). Thus, contracting muscle requires increased blood flow to support an adequate level of aerobic metabolism, while increased skin blood flow is necessary to dissipate the markedly increased metabolic heat load imposed by exercise and prevent an intolerable rise in body temperature. This competition for blood flow intensifies if either the level of work increases or if high ambient temperatures and/or humidity impair the capacity to lose heat. An extension to such competition might be anticipated for the pregnant and post-prandial states.

The physiological effects of combined heat stress and exercise on draught animals have received little attention. Therefore, this review is particularly addressed to observations on small ruminants (sheep and goats) and non-ruminants (pigs and dogs).

Effects of Exercise

General Aspects

Central cardiovascular adjustments during human exercise, and influences of the type of exercise, training, age, sex, etc., are well documented (see Rowell 1974; Saltin and Rowell 1980). In brief, cardiac output (CO) is directly related to level of exercise and thus, whole-body oxygen consumption (VO₂). However, the relation is curvilinear rather than linear because although heart rate tends to increase with VO₂, cardiac stroke volume plateaus at relatively low levels of VO₂, and may even decrease during very severe exercise. This general pattern of cardiovascular responses appears to be qualitatively similar in the dog (Barger et al. 1956; Wagner et al. 1977) and horse (Engelhardt 1977; Thomas and Fregin 1981), the only other species of large animals in which physiological and metabolic responses to graded exercise have been systematically studied.

Distribution of Cardiac Output

The major features of the redistribution of CO which occurs during exercise in humans are: increased % CO to working skeletal muscle, in proportion to exercise intensity; substantially decreased % CO to the splanchnic region and kidneys, also proportional to the severity of exercise; and decreased % CO to some other non-exercising regions, particularly torso skin and resting skeletal muscle (Rowell 1974; 1983).

These observations probably present a reasonably correct qualitative picture of exercise-induced changes in blood flow distribution in humans, but accurate quantitation remains a problem. In recent studies on other species, this problem has been largely overcome by the use of radioactive microspheres.

Working Muscle

Data from exercising dogs (Fixler et al. 1976; Pannier and Leusen 1977), pigs (Sanders et al. 1976a), horses (Parks and Manohar 1983) and sheep (Bell et al. 1983) support the accepted concept of blood flow to working muscle increasing according to its metabolic requirements and thus, level of exercise. Responses in different groups of muscles have been compared and we have estimated that in sheep doing 'moderate-to-severe' treadmill exercise (3.3 to 5.9 fold increases in VO₂ for 30 min), half the entire CO perfused muscles responsible for locomotion (Fig. 1). The degree to which...
blood flow to individual muscles increased over resting values varied from 3.6 fold (gastrocnemius) to 13 fold (biceps femoris).

![Fig. 1. Effect of exercise on distribution of cardiac output received by different groups of non-respiratory muscles (means ± SE for 5 sheep). LD, longissimus dorsi; UHL, upper hindlimb; LHL, lower hindlimb; UFL, upper forelimb; LFL, lower forelimb.](image)

ABDOMINAL VISCERA

Despite recognised methodological limitations, it seems well established that in exercising humans, blood flow to the splanchnic tissues and kidneys is decreased in proportion to the severity of the exercise (Rowell 1974). This regional vasoconstriction is necessary to make sufficient blood volume available for the vasodilator responses in other regions, however, its role in ensuring adequate flow to contracting muscles varies considerably in different species.

In the dog, absolute levels of blood flow to the kidneys and splanchnic organs are relatively unaffected, even during exhaustive exercise (Sanders et al. 1976b). On the other hand, decreases in renal blood flow have been reported for the exercising pig (Sanders et al. 1976a), and in splanchnic blood flows in exercising sheep (Bell et al. 1983). It has been argued that $V_{O_2}$ max in the dog is limited more by the metabolic capacity of skeletal muscle than by CO, and that the cardiac reserve is normally large enough to meet the vasodilator requirements without any pronounced redistribution of CO (Saltin and Rowell 1980). Thus, when CO was experimentally restricted in exercising dogs, the redistribution of CO from non-exercising organs resembled that seen in other species (Higgins et al. 1972). A comparable situation arises in the heat-stressed dog (Hales and Dampney 1975) when, in contrast to other species, thermoregulatory needs are met by increasing CO, with little change in its distribution. $V_{O_2}$ max of the dog is considerably greater than that of most other species in which effects of exercise on blood flow distribution have been measured. In another highly athletic species, the horse, renal blood flow was unaltered during moderate exercise, but decreased to 20% of resting values during very severe exercise (13 times resting $V_{O_2}$; Parks and Manohar 1983).

SKIN

Cutaneous blood-flow responses to exercise are more complex than those of other organs, presumably because skin blood flow is affected both by thermal inputs (principally deep body core temperature (Tc), modulated by skin temperature (Tsk)) and non-thermal sympathetic nervous activity (Nadel 1980; Brengelmann 1983). Absolute levels may increase during exercise in a cool or thermoneutral environment, compared with resting values, because of the effect of increased metabolic heat production on Tc.

In sheep which were at or near maximal cutaneous vasoconstriction when resting, absolute torso skin blood flow decreased significantly during exercise but was increased 7.6, 2.1 and 2.8 times in the ears, forelimb and hindlimb, respectively (Table 1). Total skin blood flow was estimated to have decreased from 169 to 136 ml/min; this represented a decrease in % CO to total skin from 5.5 to 1.9% during exercise.

OTHER TISSUES

During severe exercise, non-exercising muscles may vasoconstrict in humans (Rowell 1974), but the quantitative significance of this in terms of providing blood volume is not clear. In dogs (Sanders et al. 1976b) and sheep (Hales et al. 1984) the fraction of CO distributed to the back muscles was more or less unchanged by exercise (Fig. 1); thus blood flow to these muscles increased during walking exercise, but to a much smaller degree than in the leg muscles directly involved in locomotion.

In exercising sheep, whole-body adipose tissue received about 15% of CO during both rest and exercise, despite a 1.6–3.1-fold increase in CO during exercise (Hales et al. 1984; Fig. 2). Therefore absolute blood flow increased, which is consistent with the marked increase in adipose tissue lipolysis and fatty acid mobilisation in exercising sheep (Pethick 1982).

The increased cardiorespiratory effort required to meet increased metabolic requirements during exercise is accompanied by increases in blood flow to the respiratory muscles and myocardium approxi-
Table 1. Effect of exercise on skin blood flow in sheep (means ± SE; n = 5).

<table>
<thead>
<tr>
<th>Skin site</th>
<th>Blood flow (ml/100 g/min)</th>
<th>(% CO)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Rest</td>
<td>Exercise</td>
</tr>
<tr>
<td>Torso</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shoulder</td>
<td>8.7 ± 1.4</td>
<td>6.7 ± 1.1</td>
</tr>
<tr>
<td>Midside</td>
<td>10.0 ± 1.4</td>
<td>7.6 ± 1.3</td>
</tr>
<tr>
<td>Rump</td>
<td>13.4 ± 2.5</td>
<td>10.4 ± 1.0</td>
</tr>
<tr>
<td>Extremities</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ears</td>
<td>0.82 ± 0.1</td>
<td>6.2 ± 2.6</td>
</tr>
<tr>
<td>Forelimbs</td>
<td>1.9 ± 0.5</td>
<td>4.0 ± 1.3</td>
</tr>
<tr>
<td>Hindlimbs</td>
<td>1.8 ± 0.4</td>
<td>5.7 ± 1.5</td>
</tr>
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mately in proportion to the severity of exercise.

ARTERIOVENOUS ANASTOMOSES

We have observed up to a 5-fold increase in perfusion of arteriovenous anastomoses (AVA) of the hind limb in exercising sheep (Hales et al. 1984), which presumably is a specific response to the increased requirement for heat loss.

Effects of Heat Stress

General Aspects

Reviews of overall cardiovascular responses to heat stress in domestic animals (Hales 1974; Whittow 1976) indicate considerable species variation in the magnitude of change in CO. In cattle (Whittow 1965) and dogs (Table 2; Hales and Dampney 1975), as in humans (Rowell 1974), CO tends to increase as Tc rises. In contrast, even severe hyperthermia (>2 °C increase in Tc) has little effect on CO in sheep (Table 2; Hales 1973a) or baboons (Hales et al. 1979). Both of the major evaporative heat loss effector mechanisms, sweating and panting, require increased blood flow. Of the species discussed below in relation to detailed changes in blood flow distribution, both man and baboon rely almost exclusively on evaporative and non-evaporative heat loss from the skin, whereas the dog and sheep rely principally on evaporative heat loss from the upper respiratory passages.

Table 2. Effect of severe heat stress on cardiac output and its distribution to respiratory and non-respiratory skeletal muscles in sheep and dogs.*

<table>
<thead>
<tr>
<th>Skin site</th>
<th>Sheep</th>
<th>Dog</th>
</tr>
</thead>
<tbody>
<tr>
<td>Resp. muscles (CO/l/min)</td>
<td>TN</td>
<td>RSP</td>
</tr>
<tr>
<td>3.18</td>
<td>3.52</td>
<td>3.41</td>
</tr>
<tr>
<td>Resp. muscles (% CO)</td>
<td>2</td>
<td>14</td>
</tr>
<tr>
<td>Non-resp. muscles (% CO)</td>
<td>12</td>
<td>9</td>
</tr>
</tbody>
</table>

* TN, thermoneutral environment; RSP, peak of rapid shallow panting, Tc raised ~1°C; SDP, slow deeper panting, Tc raised ~2.5°C.
** Estimated from values for representative samples from major muscle groups.
such as the water buffalo (*Bos bubalis*), have a poorly developed capacity for sweating. Changes in skin temperature indicate marked cutaneous vasodilation during heat stress (Whittow 1962) but we are unaware of any blood flow measurements.

**RESPIRATORY MUSCLE**

Not surprisingly heat stress causes major increases in blood flow to the respiratory muscles in panting animals, in which respiratory frequency can exceed 300 breaths/min. In the sheep (Hales 1973b) and dog (Hales and Dampney 1975) blood flow to the crus muscle and diaphragm can increase as much as 10-fold, to levels never approached during maximal contraction of non-respiratory skeletal muscles. In both species % CO to the crus, diaphragm and intercostals increased from <3% in thermoneutral conditions to 10-17% during severe heat stress.

**NON-RESPIRATORY MUSCLE**

In the sheep (Hales 1973b) and baboon (Hales et al. 1979), blood flow (ml/min) to whole-body muscle decreased during mild to moderate heat stress, whereas in the dog (Hales and Dampney 1975), muscle blood flow tended to increase, although not as much as CO. In the sheep the heat-induced decline in muscle blood flow was reversed during the latter stages of severe heat stress, when Tc had increased by more than 2°C and slower, deeper panting and respiratory alkalosis prevailed.

**ABDOMINAL VISCERA**

Major decreases in renal and splanchnic blood flows have been observed in the heat-stressed sheep (Hales 1973a) and baboon (Hales et al. 1979). This redistribution of blood flow assumes added significance because, as noted earlier, CO is relatively unaffected by heat in these species. In contrast, the dog appears to rely mainly on increased CO to supply the increased blood flow requirements of the respiratory muscles and skin. Nevertheless, relatively unchanged renal and gastrointestinal flows in the face of increased CO could be regarded as a form of redistribution of blood flow, since % CO to these organs clearly decreased during severe heat stress (Hales and Dampney 1975).

**ARTERIOVENOUS ANASTOMOSES**

Under thermoneutral conditions in which skin vasodilation is minimal about 2% of CO in sheep appears to pass through AVAs, most of which are probably located in skin, but during heat stress this fraction can exceed 10% CO (Hales 1983a). In the dog and baboon about 5 and 9% of CO, respectively, bypasses the systemic capillary circulation during heat stress.

**Combined Effects of Exercise and Heat Stress**

The nature of the cardiovascular problems posed by the combination of exercise and heat stress has been extensively studied in human subjects (see reviews by Rowell 1974, 1983; Nadel 1980). These problems have not been examined although they are potentially important for draught animals, the great majority of which have to work in the tropics. In smaller ruminants, the only detailed studies appear to be those of Bell et al. (1983) on sheep and Feistkorn et al. (1984) on goats.

**Humans**

In humans, the capacity for increasing CO at a given level of upright exercise in hot versus cool environments is limited, because several factors operate to reduce central blood volume and thus, venous return to the heart and stroke volume. These include: a major increase in the volume of blood in skin; decreases in blood plasma volume due to increased capillary filtration in contracting muscle; and loss of body fluid in sweat. Since further major increases in CO are clearly out of the question, any heat induced modifications to the distribution of CO during exercise assume a critical importance as the only remaining major strategy for maintaining both circulatory and thermal stability during physiologically tolerable combinations of exercise and environmental heat.

Exercise-induced decreases in splanchnic and renal blood flows are greater in hot than in cool environments, but the combined reductions in these...
flows during moderate to heavy exercise in the heat are unlikely to provide sufficient blood for sweating skin and/or exercising muscle (see Rowell 1974). More recently, it has been shown that skin is relatively vasoconstricted under these conditions (Johnson et al. 1974; Brengelmann et al. 1977; Nadel et al. 1979). This vasoconstrictor response appears to be the mechanism for avoiding the circulatory collapse which would presumably occur if accumulation of blood in cutaneous capacitance vessels continued unabated simply to meet thermoregulatory demands. The relation between Tc and skin blood flow during heat exposure is also modified by state of hydration. Hypohydration of human subjects during exercise in the heat, which decreased stroke volume and CO, caused an elevation in the Tc threshold for cutaneous vasodilation and reduced maximal skin blood flow by about 50% (Nadel et al. 1980). Blood flow to exercising muscle may also be compromised by competition with skin (Rowell 1974; 1977), but direct evidence in humans is lacking.

**Sheep and Goats**

The circulatory consequences of combined heat and exercise stresses in these species might be expected to be less drastic than in humans for several reasons; firstly, the sheep does not distribute nearly as large a fraction of its CO and blood volume to skin as does man; secondly, venous return of the quadruped will be much less affected by gravity than that of upright man, under any conditions; and thirdly, ruminants have a considerably larger gut from which to redistribute blood flow than does man and other non-ruminants. This has been borne out by our observation that CO, heart rate, mean arterial pressure and total peripheral resistance were not significantly affected in sheep exercising in a hot (40°C) environment. Changes in rectal temperature, V̇O₂ and CO under these conditions are shown in Fig. 3. Effects of Tc have been examined more specifically in goats exercising at 35°C, with their body temperatures clamped at 39°, 40.5° or 42°C (Feistkorn et al. 1984). Once again there was
little effect of Tc on central cardiorespiratory parameters.

In contrast to the gross cardiovascular parameters, exercise-induced changes in the distribution of CO in sheep were altered considerably by heat exposure (Fig. 2; Hales et al. 1984). In particular, there was a major decrease in the fraction of CO going to non-respiratory muscles. This decrease amounted to about 1600 ml/min, which was more than sufficient for both the decrease in CO and increases in flow to respiratory muscles (for panting) and skin. Thus, a 'balanced' cardiovascular response was actually measured—something not previously done in man or other species.

Several other features of Fig. 2 warrant comment. Surprisingly, and in contrast to humans, % CO to the kidneys was actually significantly higher during exercise in MH compared with exercise in TN. Absolute renal blood flow was also significantly increased. We have no explanation for this apparent failure to redistribute the available blood volume, unless this renal flow is needed for renal compensation of the respiratory alkalosis which can develop in panting animals. Also in contrast to humans, there was no further decrement in % CO to any of the splanchnic tissues. In addition, the estimated fraction of CO perfusing adipose tissue was unaltered during exercise in the heat.

The results summarised in Fig. 2 do not indicate whether working or resting muscle, or both, were sites of decreased blood flow during MH. However, when % CO to individual muscle groups was compared it became apparent that most, if not all, of the decrease was confined to locomotory muscles in the limbs. In contrast, % CO to torso muscles was quite unaffected. We do not know whether decreased blood flow was accompanied by reduced metabolism in exercising muscle. However, in sheep undergoing a similar level of exercise in thermoneutral conditions, there was a substantial reserve in the oxygen content in venous blood draining the active hindlimb, which was greater than 40% of arterial oxygen content (Bird et al. 1981).

Exercise and Heat Stress During Pregnancy

Physiological responses to exercise during pregnancy have been recently reviewed (Lotgering et al. 1985). In pregnant ewes, moderate to severe treadmill exercise caused a 20–40% decline in uterine blood flow (Clapp 1980; Chandler and Bell 1981; Lotgering et al. 1983a; Bell et al. 1984; Chandler et al. 1985). This was associated with the development of moderate fetal arterial hypoxaemia, which persisted during maternal exercise, but usually disappeared soon after exercise ceased (Chandler and Bell 1981; Lotgering et al. 1983b). A more serious consequence of maternal exercise may be the elevation, and slow decline during recovery, of fetal Tc (Lotgering et al. 1983b; Fig. 4), as the duration of a
Prolonged heat exposure during mid and late pregnancy causes fetal growth retardation in sheep (Alexander and Williams 1971) and cows (Reynolds et al. 1985). This could be attributed to a decreased uterine blood flow, which has been observed in sheep exposed to severe heat stress for several hours (Oakes et al. 1976; Brown and Harrison 1981) or more importantly, during mid pregnancy, in ewes (G. Alexander and J. R. S. Hales, unpublished data) and Hereford cows (Reynolds et al. 1985) chronically exposed to levels of environmental heat commonly encountered in tropical countries (Table 3). In ewes returned to a cool environment in late pregnancy, after heat exposure between 50 and 120 days of gestation, both uterine and umbilical blood flows were permanently reduced (A. W. Bell and G. Meschia, unpublished data).

Late pregnant ewes stressed by exercise and mild heat (Td = 40°C) appeared to cope as well as their non-pregnant counterparts (Bell et al. 1983; 1984). Although they developed a greater degree of hypocapnoea and respiratory alkalaeama than during exercise in a cool environment, the exercise-induced decrement in uterine blood flow (~30%) was unchanged by heat exposure (Bell et al. 1984). Also, the effects of heat exposure on exercise-induced changes in blood flows to exercising muscles and visceral tissues, observed in non-pregnant sheep (Bell et al. 1983), were largely absent in pregnant ewes. This suggests that the substantial fraction of uterine blood flow which is available for redistribution may actually enhance the capacity of the pregnant animal for exercise. However, prolonged work, particularly in the heat, is likely to have deleterious effects on fetal oxygenation, body temperature and growth (see Lotgering et al. 1985).

### Limits to Work Output in Hot Environments

What limits the ability of animals to work in the heat, and how is this related to conflicting requirements for the distribution of blood flow? In humans, it seems reasonably clear that a major limiting factor is the threat of circulatory collapse, for which a degree of cutaneous vasoconstriction is an attempted compensation but exacerbates the hyperthermia. In the goat, which is a panting animal, circulatory integrity appears to be less threatened and it has been suggested that temperature-dependent accumulation of lactic acid in exercising muscle may limit the ability to exercise during heat exposure (Feistkorn et al. 1984). This could be related to muscle hypoxia, associated with the smaller degree of exercise hyperaemia in the heat (Bell et al. 1983). Alternatively, lactate production and/or release by muscle may have been stimulated by respiratory alkalosis, the depth of which increases with Tc.

The capacity of the evaporative heat loss mechanisms is smaller in panting than in sweating species (Taylor 1977). The ability to lose heat by panting is probably limited by the metabolic rate and/or biomechanical properties of the respiratory muscles rather than their blood supply, since their blood flow rate (Hales 1973b) is markedly higher than that ever reported for exercising muscles and the fraction of CO involved is low relative to, say,
that going to skin in man under similar conditions. Although the overall metabolic cost of panting is relatively low at rest, at least in sheep and cattle, this is only because of concomitantly reduced metabolism in tissues other than the respiratory muscles (Hales and Brown 1974); this could not occur during severe exercise without some penalty.

Physiological limits to working ability in tropical draught animals have not been systematically studied. Species differences in the relative importance of sweating and non-sweating mechanisms for heat dissipation could be important. For example, in Zebu (Bos indicus) cattle sweating is considerably more important than panting (MacFarlane 1968), whereas the water buffalo is poorly supplied with sweat glands and needs to wallow to assist cutaneous evaporative heat loss. Not surprisingly, buffaloes became stressed much more quickly than Indian cattle when exposed to intense solar radiation (Mullick 1960).

Within a given species and breed, a number of other factors and their interactions are likely to affect working ability in hot environments. These include a possible interaction between physical training and heat tolerance, as observed in humans (Roberts et al. 1977), and effects of feed and water intakes. For instance, the ability to endure enforced walking in a hot environment was lower in Hereford steers on a high plane of nutrition than in those fed to lose weight (Murray et al. 1981). Further, exercise-induced increases in Tc were found to be greater in steers on a restricted water intake and, although this did not appear to be caused by decreased sweating rates (Schmidt et al., 1980), water restriction will commonly reduce cutaneous vasoconstriction, sweating and panting ability.

References


Hales, J. R. S. 1973a. Effects of exposure to hot environment on the regional distribution of blood flow and on cardiorespiratory function in sheep. Pflugers Arch. 344: 133.


Changes in Body Temperature and Working Efficiency of Thai Swamp Buffalo

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BUFFALO have been of economic importance in Thailand for centuries. According to the Agricultural Statistics of Thailand in 1982, there were 6.4 million head in the country, with 60% in the Northeast. Most Thai farmers raise buffaloes, primarily draught animals, for ploughing their croplands. The use of buffalo for draught is quite suitable economically and socially, especially for farmers who live in remote areas and who own only small parcels of land and family labour is available when needed. Although many farmers would prefer to use machinery, the shortage of petroleum products demands that renewed attention be directed to the use of buffalo power in Thailand.

Drought resulting from inadequate amounts or poor distribution of rainfall is a serious problem in many areas of Thailand. There are, however, supplies of water available in natural sources such as streams, ponds or in aquifers at shallow depths. Economical methods are needed for lifting such water and distributing it to sites where it could be used effectively. Buffaloes may have an important role in providing such power rather than using gas-powered machines. Little or no research has been done on this problem, although buffaloes are still used with old water-lifting devices in some areas such as Lampang Province in Northern Thailand.

The present effort is to study the use of buffaloes for the operation of a water-lifting device. The aims of this research are: (1) to study the buffalo behaviour while operating the water-lifting device; (2) to study the changes in body temperature of buffalo within one working hour; (3) to study the efficiency of buffalo power for operating the water-lifting device; and (4) to study the efficiency of buffaloes during different periods of time during the day.

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Literature Review

Although the buffalo has been used as a draught animal for a very long time in Thailand, very little research has been done in this area. A study on the physiological consequences in the buffalo resulting from work has not yet appeared, but it is, however, relevant to review the physiological conditions and the working ability of Thai swamp buffalo here.

Physiological Characteristics

Very little research on the physiology of Thai swamp buffaloes has been conducted.

Harber (1980) studied 42 newborn calves in the northeastern villages of Thailand. He found that the average body temperature was 38.6°C, the pulse rate 177.8/min, and the respiration rate 59.2/min. Harber and Usanagornkul (1981) reported the body temperature of 65 newborn calves at Surin Buffalo Research Center which was not different from the former (38.5°C). It was also observed that the value could rise physiologically to an average of 40.1°C after sunbathing and after a long walk (about 1.5 km) from the pasture to the night corral.

Chantaraprateep and Bodhipaksa (1975) observed the general body condition of six male buffaloes aged 3-5 years of age. The same parameters were examined by Teinkhao and Teinkhao (1978) in mature buffalo bulls. The average values of respiration rate, pulse rate, and body temperature were 20/min (167 animals), 30/min (165 animals), and 37.7°C (80 animals) respectively.

Climatic Effects

Heat Tolerance

While the buffalo is remarkably versatile, it has poorer physiological adaptation to extremes of heat and cold than the various breeds of cattle. Body temperatures of buffaloes are actually lower than
those of cattle, but the buffalo skin is usually black and heat-absorbent and only sparsely protected by hair. Also, buffalo skin has one-sixth the density of sweat glands that cattle skin has, so buffaloes dissipate heat poorly by sweating. If worked or driven excessively in the hot sun, a buffalo's body temperature, pulse rate, respiration rate, and general discomfort increase more quickly than those of cattle. Buffaloes prefer to cool off in a wallow rather than seek shade. They may wallow for up to 5 hours/day when temperature and humidity are high (NRC 1981).

Recent Studies in Thailand

The comparative study of physiological characters of swamp buffaloes between two different time periods was investigated by Sripongpun (1976). The number of animals used was six females, 3-4 years of age, kept in an open-shed barn. The mean of respiration rate at noon was not different from the evening (30.7 vs 30.9/min), while the pulse rate and the body temperature in the evening were significantly higher than at noon (56.3 vs 49.7/min and 39.1 vs 38.4°C).

Chaiyabutr et al. (1983) reported the effect of heat exposure on physiological changes of swamp buffaloes, 3-4 years of age. The buffaloes were exposed to the summer sun (April-July) for 4 hours. The respiration rate began to increase by 52% by the first hour and by nearly four times on the fourth hour. It was observed that the heart rate relative to respiration rate increased very little after 1 hour of sun exposure, but significantly increased after 4 hours. Rectal temperature of buffalo rose from 38.9°C to 40.4°C after 4 hours of sun exposure.

Pruksasri (1983) studied the diurnal changes of three physiological responses of swamp buffaloes to the ambient temperature and compared them with similar data for cattle. It was found that changes in body temperature, respiration rate, and pulse rate of buffaloes significantly positively correlated with the changes of ambient temperature. In cattle, the relationship between the ambient temperature and body temperature was significantly positive, but that the pulse rate was not significant, and the respiration rate was negative.

Working Ability

The greatest numbers of buffaloes in Thailand are used for draught mainly in rice production; for ploughing and harrowing the paddy fields, for rice threshing and milling, and for transportation. In some areas, farmers used them to turn sugarcane crushers and water-lifting devices. Buffaloes are well suited to work in muddy and submerged fields where they are able to pull heavier loads than cattle (Chantalakhana 1975). Training buffaloes for work begins at the age of 3-4 years. Most Thai buffaloes work for 5 hours a day, each plough about 0.1 hectare per day (Buranamanus 1963; Rimkiree 1984). Their hard working period is from May to September, which is the rice-growing season (Buranamanus 1963). Therefore, the shortage of buffalo power usually occurs during that period (Ratanadilok Na Puket 1979). Cockrill (1974) compiled information concerning the working periods of buffaloes in certain regions of Thailand. It was found that buffaloes worked from 66 to 146 days per year (average 122).

A very recent study by Konanta et al. (1984) reported the working performance of Thai swamp buffalo compared with crossbred Murrah under feed supplementation at Surin Buffalo Research Center. The former seemed to work better than the latter as shown by the results of area ploughed and walking speed.

Besides the reports on working ability of buffalo in the paddy fields, its efficiency in pulling a cart and turning a sugarcane crusher in terms of speed has been studied (Rimkiree 1984).

In addition, Chantalakhana (1983) stated that most reports available in the past gave only general working ability of buffalo (Rife and Buranamanus 1959; Buranamanus 1963; De Boer 1971; Rufener 1971; Bhannasiri 1975; Monkonpunya 1978; Niumsup and Songprasert 1978).

Present Study

Buffalo

Four male buffaloes used in our research belonged to the Rice Division, Department of Agriculture. They were raised for ploughing land which is used for experimental rice plantings. Their weights, estimated by measuring heart girth (Ratanarochanchart 1974) were 656, 674, 608 and 608 kg, respectively. The animals were approximately 20 to 25 years old. Their feed is usually obtained from natural grass where stockmen drive them to graze along both sides of the roads. When the weather is very hot, the buffaloes may wallow in water ways, taking water hyacinth as their feed. During the trials, silage was provided for the animals.

Water-Lifting Device

The water-lifting device used in these trials was constructed by Thai engineers and consists of two units: the pump and the transmission (Fig. 1). The construction materials used to make this device were those which would be readily available in rural areas.
The water-lifting device operated by buffalo power was installed on the bank of a ditch in the area of the Rice Division, Department of Agriculture, on the east side of Suwanwajokkasikit Road. The study period was about 3 months (April 18 to July 20, 1983).

PROCEDURES

1. The animal harness system to operate the water-lifting device was to place the free end of the power lever atop the neck of the buffalo. A rope was tied to the end of the lever, then passed under the neck of the buffalo and tied to the lever on the other side of the neck. Care was taken to be sure the rope was not too tight. The buffalo was directed to walk in a circle by the stockman who followed behind and outside the path of the animal. Before collecting data, each animal was trained on 2 or 3 occasions for periods of 30 min.

2. Four 1-hour work periods during a day were set as follows: 7.30-8.30, 9.00-10.00, 1.30-2.30; and 3.00-4.00 pm. The buffaloes worked in each of the four time periods. While working, revolutions/min and steps/min were recorded in the first and the second half of each hour.

3. The buffalo body temperatures were measured before and after 1 hour of work using a rectal thermometer. The ambient temperature was also recorded.

4. The buffalo behaviour was observed during each working hour.

DATA ANALYSES

1. Changes in body temperature and the efficiency of individual animals in the first and the second half of an hour were analysed by paired comparison (Chantalakhana 1976).

2. Analysis of variance was used to test the significance of differences of working efficiency of buffaloes in different time periods during a day. The design involved samples within samples, with unequal sample sizes (Chantalakhana 1976).

Results and Discussion

Buffalo Behaviour

When the buffaloes were first required to walk in a circular pattern, they reacted adversely and became very difficult to handle. Therefore, they had to be trained by a very skilled stockman or operator under whom they could be controlled. He used a stick lightly on their hind quarters to encourage them to follow the correct course until they became familiar with it.

During the first 15 days, the experimental buffaloes, generally, groaned and slavered as they worked. Often they stopped walking and opened their mouths widely. This was especially true during the last 30 min of a working hour. Some tried to gore the lever, resisting the requirement to walk in a circular direction. Strangers passing close to the animals always frightened them. After about 15 days, the buffaloes became accustomed to the pattern of the experiment, and their strange behaviour largely disappeared.

The four experimental animals have been used for ploughing paddy fields for a long time. They responded only to the orders of the two stockmen who have raised them for over 20 years. According to these stockmen, these animals could be rated as being highly efficient animals for ploughing. While ploughing they were accustomed to walking in a straight path, whereas in this experiment they were forced to walk in a circle to move the water-lifting device. Their adverse reactions appeared to be because of unfamiliarity with the pattern. Groaning
Table 1. Changes in body temperature and working efficiency of individual buffalo operating the water lifting device (X ± SD).

<table>
<thead>
<tr>
<th>Buffalo number</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weight (kg)</td>
<td>656</td>
<td>674</td>
<td>608</td>
<td>608</td>
</tr>
<tr>
<td>No. of observations</td>
<td>32</td>
<td>13</td>
<td>59</td>
<td>25</td>
</tr>
<tr>
<td>Ambient temp. (°C)</td>
<td>34.01 ± 5.22</td>
<td>36.67 ± 5.50</td>
<td>33.43 ± 4.07</td>
<td>33.84 ± 3.43</td>
</tr>
<tr>
<td>Body temp (°C)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Initial</td>
<td>38.06 ± 0.17</td>
<td>37.73 ± 0.63</td>
<td>37.99 ± 0.17</td>
<td>38.04 ± 0.14</td>
</tr>
<tr>
<td>Final</td>
<td>39.03 ± 0.12</td>
<td>38.54 ± 0.63</td>
<td>39.00 ± 0.21</td>
<td>39.00 ± 0.0</td>
</tr>
<tr>
<td>Difference</td>
<td>0.97**</td>
<td>0.81**</td>
<td>1.01**</td>
<td>0.96**</td>
</tr>
<tr>
<td>Revolutions/min</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st half</td>
<td>2.84 ± 0.26</td>
<td>3.65 ± 0.44</td>
<td>3.10 ± 0.38</td>
<td>2.91 ± 0.41</td>
</tr>
<tr>
<td>2nd half</td>
<td>2.83 ± 0.30</td>
<td>3.58 ± 0.45</td>
<td>3.20 ± 0.37</td>
<td>2.99 ± 0.30</td>
</tr>
<tr>
<td>Difference</td>
<td>0.01ns</td>
<td>0.07ns</td>
<td>-0.10*</td>
<td>0.08ns</td>
</tr>
<tr>
<td>Steps/min</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st half</td>
<td>66.80 ± 5.79</td>
<td>68.54 ± 21.72</td>
<td>70.45 ± 7.22</td>
<td>64.36 ± 5.49</td>
</tr>
<tr>
<td>2nd half</td>
<td>66.31 ± 4.91</td>
<td>74.81 ± 8.22</td>
<td>71.43 ± 7.48</td>
<td>65.98 ± 6.32</td>
</tr>
<tr>
<td>Difference</td>
<td>0.49ns</td>
<td>-6.72**</td>
<td>-0.97ns</td>
<td>-1.62*</td>
</tr>
<tr>
<td>Average step length (m)</td>
<td>0.67</td>
<td>0.79</td>
<td>0.70</td>
<td>0.71</td>
</tr>
<tr>
<td>Average speeda (km/hr)</td>
<td>2.67</td>
<td>3.40</td>
<td>2.97</td>
<td>2.78</td>
</tr>
</tbody>
</table>

a The lever length from centre of the base to the middle point of the neck of the buffalo is 2.5 m.

ns = non significant, * = significant at 5% level, ** = significant at 1% level.

and slavering may be signs of uneasiness. Opening the mouth widely may be a way to take in more oxygen. The harness used was also different from that used in pulling the plough. Some animals adjusted rather easily, while others were quite disturbed and tried to gore the lever. However, all animals later worked well within the time set.

Changes of Body Temperature

Working during 1 hour of exposure to the sun caused temperatures of all four buffaloes to rise (P 0.01) 0.97°, 0.81°, 1.01 and 0.96°C, respectively (Table 1). Similarly, Chaiyabutr et al. (1983) reported from an experiment in Thailand that after 4 hours direct sun exposure temperatures of buffalo rose every hour from an initial reading of 38.94°C to 39.17, 39.56, 40.17, and 40.39°C, respectively. During one trial in Egypt, 2 hours of working exposure to the sun caused temperatures of buffaloes to rise 1.30°C (NRC 1981).

Efficiency of Buffalo Power

The working efficiency of four buffaloes was compared as shown in Table 1. The revolutions/min of three buffaloes between the two halves of a working hour were not significantly different (2.87 vs 2.83, 3.65 vs 3.58, 2.91 vs 2.99), while for one buffalo there was a significant increase from 3.10 to 3.20. The numbers of steps per minute were also compared. Two animals had no significant change in the two halves (66.80 vs 66.31 and 70.46 vs 71.43). One animal had more steps/minute in the second half (64.36 vs 65.98). The fourth animal had a highly significant increase in the second half (68.54 vs 74.81).

These results showed that buffaloes worked well in a whole period of 1 hour. Some individuals walked faster in the second 30 min. Therefore, buffaloes were able to work without any break for 1 hour while operating the water-lifting device. Further experiments should be conducted over periods longer than 1 hour to get more information on the efficiency curve.

In this study, the average walking speed and the average length of step for the four buffaloes were 3.08 revolutions/min or 2.9 km/hour, and 0.7 m, respectively. Similarly, Rimkiree (1984) observed buffaloes walking in a circular pattern to turn a sugarcane crusher at an average speed of 3.0 km/hour.

The relative efficiency of buffalo in four different time periods during a day was calculated in terms of revolutions/minute and steps/minute. Differences were not significant (Table 2), however, the results indicated that buffaloes worked more efficiently in the morning than in the afternoon. This observation agrees with farmer experience since they generally use the buffaloes to plough in the morning while the temperature is cooler and let them graze and wallow in the afternoon. Chantalakhana (1981) had also stated that working efficiency of buffaloes
was affected by heat. They like to wallow in water, and particularly in mud, when the temperature is high. In shade or in wallow buffaloes cool off quickly, perhaps because a black skin rich in blood vessels conducts and radiates heat efficiently (NRC 1981).

### Conclusion

From a thorough review of work done in Thailand on physiological changes in buffalo, including this investigation, we conclude that much research remains to be done in this area. Future priority research in Thailand, therefore, should emphasise basic physiological studies in working buffalo and cattle.

### References


Buranamanus, P. 1963. A survey of the buffalo in Thailand, Faculty of Veterinary Science, Kasetsart University, Bangkok, Thailand.


De Boer, A. J. 1971. Factors affecting the output of cattle and buffalo in selected areas of Thailand. Proceedings of the National Conference on Agricultural and Biological Science. 10th Session, Kasetsart University, Bangkok, Thailand.


Ratanadilok Na Puket, S. 1979. The role of swamp buffalo in small farm development. FFTC/ASPAC Seminar paper on Increasing Buffalo Production for Small Farms, Kasetsart University, Bangkok, Thailand.


Physiological Changes Associated with Work: Some Lessons from the Horse

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Much of the information available on the physiology of exercise has been obtained, not surprisingly, from studies on animals involved in leisure sports. Physiological changes associated with exercise and repeated exercise are reasonably well documented for the athlete and the racehorse, the elite well-nourished performers. More recently with the popularity of marathon running and endurance riding the effects of prolonged exercise on the average performer have also been studied. Although there are many more animals kept for draught purposes than for competition throughout the world, there is little information available on exercise in draught animals. This is particularly true of the draught ruminant, possibly regarded as the poor relation of the racehorse. Unlike the racehorse or athlete it is not always well fed and often has to work for long periods of time at high environmental temperatures.

In this article factors influencing an animal's ability to do work are examined and some of the physiological consequences of exercise are discussed, drawing on information obtained from the study of equine exercise physiology. The application of physiological measurements to draught animals is considered in the final section.

Metabolic Factors Affecting Work Capacity

In its role as a power source in agriculture and transport a draught animal can be thought of as a 'machine' which converts chemical energy into mechanical energy. At the same time other functions such as maintenance, growth and milk production compete for the energy supply. Conversion of chemical to mechanical energy is accomplished by muscle tissues. The success with which the animal carries out this process will depend on its ability to supply energy to the tissues and to use it.

Energy for Muscle Contraction

The immediate source of energy for muscle contraction is ATP. The energy released is used directly by the contractile mechanism:

\[ \text{ATP} + \text{H}_2\text{O} \xrightarrow{\text{myosin ATPase}} \text{ADP} + \text{Pi} + \text{H}^+ + \text{Energy} \]

The concentration of ATP in skeletal muscle is very limited and if muscle contraction is to continue for more than a second or two ATP must be resynthesized. This resynthesis is achieved by two distinct processes, aerobic phosphorylation and anaerobic phosphorylation.

Aerobic Metabolism

At low work rates (submaximal exercise) energy is provided by aerobic metabolism of substrate (largely NEFAs) using oxygen provided by the blood circulation. The rate of oxygen transport to the tissues can meet the demand and ATP used up during muscle contraction can be replenished by aerobic phosphorylation. This involves the reduction of substrates from fat and carbohydrate metabolism and their subsequent oxidation in the TCA cycle in mitochondria. Aerobic metabolism is a relatively slow process because of the complexity of the reactions and the cardiovascular delay in supplying oxygen. It can take up to 60 sec to reach full aerobic production (McMiken 1983), however the yield of energy is high. The oxidative production of ATP from glycogen yields 36 moles of ATP per mole of substrate.

Anaerobic Metabolism

At high work rates (maximal exercise), rate of muscle contraction or degree of contraction is increased as more muscle fibres are activated. The maximum rate at which oxygen can be supplied to the muscle cells is exceeded and the aerobic energy pathways can no longer entirely meet the demand. In this situation, anaerobic regeneration of ATP from creatine phosphate, ADP and the conversion of pyruvate to lactate during anaerobic glycolysis provides additional energy at a rapid rate (within 1 sec) to the muscle cells. The energy yield from this process is much lower than that from oxidative processes. From glycolysis the yield is only 2 or 3...
moles ATP per mole of substrate (depending on the substrate) and for creatine kinase and myokinase the yield is only 1 mole ATP per mole of substrate used. The rapid provision of energy cannot be sustained for long as anaerobic substrates notably glycogen and glucose are soon depleted and work rate has to decrease. Hence maximal effort can be reached rapidly but cannot be sustained. Even the horse which has a high glycogen storage capacity can maintain top speed for only about 800 m when galloping (McMiken 1983).

**Physiological Work Capacity**

In the exercising animal aerobic and anaerobic metabolism proceed simultaneously. All energy pathways are used in the muscle to some degree at all workloads. At low rates muscle lactate is oxidised by neighbouring fibres or removed by gluconeogenesis so blood lactate does not increase beyond an initial equilibrium. With increased work rate there is a point at which lactate concentrations increase progressively because the production of lactate exceeds its removal from the bloodstream. This point has been defined as the anaerobic threshold.

Draught animals are generally believed to perform work at submaximal exercise levels well within the limits of aerobic metabolism. However, short-term increases in work rate are often required—e.g. when moving off with a laden cart, freeing an implement from rough ground or working uphill—when the animal may operate at maximal level, making demands on its energy reserves during increased anaerobic metabolism. This may lead ultimately to fatigue and reduced work output during the day if the energy reserves are not ‘topped up’.

Clearly the more effective the aerobic metabolism is the greater will be the reserves of anaerobic energy available. These reserves may be used gradually to enable the animal to work at a higher average rate over an extended working period or saved for a maximum effort over a short period. In either case the animal will work better than if it has to use the limited reserves merely to maintain low work output.

**Energy Supply and Utilisation**

The main factors influencing energy supply and utilisation in aerobic and anaerobic metabolism are given schematically in Fig. 1. Anything that increases energy supply (e.g. training or nutrition) must increase an animal’s work capacity. However, and equally true, anything that has a detrimental effect (e.g. disease) can reduce physiological work capacity. Basic physiological mechanisms such as muscle contraction, energy metabolism, respiration, circulation and heat dissipation are essentially the same in most mammals. It is the quantitative aspects which determine the differences in the supply and use of energy by the tissues doing work.

**Non-Physiological Factors Affecting Work Output**

Physiological limitations are not the only factors limiting the ability of an animal to perform work. Psychological and physical characteristics and environmental factors must also be taken into consideration when relating physiological changes to the amount of work done. Temperament and training have a considerable effect on the amount of work an animal accomplishes. Coordination, gait and muscular strength, influenced by the size and conformation of the animal, similarly affect work output. Environmental conditions, terrain, soil type, design of implement and the motivation of the driver and his experience in handling animals also influence the work achieved during a particular period.

**The Horse or the Ruminant for Work?**

The horse is the only large working animal in which physiological and metabolic responses to
graded exercise have been studied in any detail (e.g. Snow et al. 1983). Measurements of cardiovascular and respiratory responses to exercise, detailed studies of blood and muscle metabolites and more recently studies of muscle types have enabled the physiological changes associated with a range of different activities to be studied. Observations have shown that the horse, because of certain physiological advantages, has probably the greatest capacity for physical work of all domestic animals.

The advantage of the horse over other working animals is its unique ability to greatly increase the oxygen carrying capacity of its blood during exercise. The horse is capable of storing one-third to one-half of the total red cell volume in the spleen. Splenic contraction occurs in response to the sympathetic stimulation caused by exercise (Persson and Bergsten 1975), haematocrit and haemoglobin concentrations are elevated and the total circulating red blood cells can be increased by as much as 50% (Persson 1967; Thomas and Fregin, 1981). This enables the horse to increase its aerobic metabolism by up to 36 times during strenuous exercise (Thomas and Fregin 1981) compared with the two-fold increase observed in man (Astrand 1976) and the dog (Wagner et al. 1977). In addition, equine muscle has a high capacity for glycogen storage (over 126 mmol/kg) which provides considerable reserves for anaerobic metabolism (McMiken 1983). Glycogen reserves in skeletal muscles of cattle are lower, largely because the ruminant is dependent on hepatic gluconeogenesis of volatile fatty acids to provide most of the glucose and glycogen reserves (Judson et al. 1976), unlike the horse in which most glucose is absorbed directly from the gut. This does mean that the ruminant can survive on relatively high-energy diets whereas the horse, particularly when working, requires low-energy feeds if it is to maintain performance. In fact diminished endurance in grass-fed horses is a common observation.

The horse, like other animals, the dog (Wagner et al. 1977) and man (Smith et al. 1976) can increase cardiac output up to 5- to 6-fold in response to exercise (Persson 1967; Bergsten 1974; Thomas and Fregin 1981). However this does not entirely determine the delivery of blood to the working muscle because the requirements of other tissues have to be met. The need to supply blood to the skin for heat dissipation may constrain aerobic metabolism during exercise and has been observed to limit endurance performance in horses during events which lasted for several hours (Carlson and Mansmann 1974; Rose et al. 1979; Lucke and Hall 1980). The horse relies on evaporative loss by sweating as the main means of heat dissipation. Consequently a substantial loss of electrolytes and dehydration can occur during prolonged exercise (Rose et al. 1980a; Snow et al. 1982). Dehydration in the ruminant, which places less reliance on sweating, may be less of a problem particularly with the large but unpredictable reservoir of water in the rumen.

Bearing in mind the differences between the horse and ruminant during exercise, data from research on the horse may be helpful in determining which measurements to use in draught animal studies.

Changes Associated with Prolonged Exercise

Low blood glucose and high plasma NEFAs during endurance exercise in the horse (Rose et al. 1977; Snow and Mackenzie, 1977a; Lucke and Hall 1980) are consistent with NEFAs being the major energy source in prolonged exercise. Little change in lactic acid levels occur after the initial rise due to early glycolysis (Snow and Mackenzie; 1977a; Lucke and Hall, 1980; Dybdal et al. 1980). In fact alkalosis is a feature of prolonged exercise rather than the metabolic acidosis associated with maximal exercise (Snow and Mackenzie 1977b). The former is probably caused by increased ventilation associated with the need to aid heat dissipation (Snow and Mackenzie 1977a). Plasma corticosteroids increase while insulin concentrations decrease during prolonged exercise (Dybdal et al. 1980). The anaerobic threshold is only reached in activities using sudden intense efforts such as polo (Craig et al. 1985) and 3-day eventing (Rose et al. 1980b), and is associated with a marked increase in plasma lactic acid concentrations. Detailed observations of biochemical changes in blood before and after training at submaximal levels have not shown any consistent changes in parameters which could be used to determine fitness (Snow and Mackenzie 1977a; Rose and Hodgson 1982) although training at maximal levels appears to improve the utilisation of glycogen and NEFA as substrates by working muscle (Snow and Mackenzie 1977b). Similarly, no consistent differences have been observed in the blood parameters of those horses that completed an endurance exercise compared with those that failed (Dybdal et al. 1980). Rose and Hodgson (1982) concluded that routine haematological and biochemical screening had no useful role in assessing the fitness of endurance horses.

Muscle Fibre Types

The evolution of distinct muscle fibre types in mammalian limb muscles effectively provides a gearing system minimising the energy cost of locomotion (Alexander and Goldspink 1979). Studies using muscle biopsy sampling with biochemical and histochemical techniques have provided information on the utilisation of substrates in specific
fibre types in horses during prolonged exercise. Different types of fibre have been identified.

**TYPE I**

Known as slow twitch fibres, Type I have a contractile time about three times longer than fast twitch fibres. Histologically they are rich in mitochondria and oxidative enzymes, and designed for a high rate of aerobic energy production. They are high in myoglobin content and have extensive capillaries which facilitate oxygen diffusion. The high energy yield and utilisation of oxygen give the Type I fibres great endurance qualities.

**TYPE II**

Histochemical staining has identified three types of Type II myosin ATPase in fast-contracting muscle which are designated Type IIA, IIB and IIC (Brooke and Kaiser 1970). Type IIA has fast-contracting properties but is also well equipped for oxidative energy production and therefore has good endurance properties. Type IIB fibres yield high rates of energy from intramuscular stores, having a high rate of energy release but limited endurance capacity. Type IIC fibres are present in only a small proportion, being more evident in very young animals. They seem to be a transitional stage in the development of new fibres and contain both fast and slow myosin (Snow et al. 1981a).

The different fibre types occur in different proportions in the various skeletal muscles. In addition the proportions of fibre types in a particular muscle vary between individual animals. The proportion of Type I and Type II fibres appears to be genetically determined and not altered by normal physiological adaptations. Snow and Guy (1980) studied the fibre composition in six limb muscles of different breeds of horse. They found the percentage of fast twitch fibres in the m gluteus medius varied significantly amongst breeds and these differences were related to the sprinting speed of the breed. The quarter horse had the highest percentage, followed by the thoroughbred, with the donkey and heavy hunter having the lowest proportions. Similarly some of the muscle enzymes activities could be related to the performance for which the animals were best suited. The quarter horse had the highest activity of the glycolytic/anaerobic enzymes and the glycolytic related enzymes (lactic dehydrogenase, aldolase and glycero1-3-phosphate dehydrogenase) and among the lowest activities of aerobic enzymes (citrate synthase, 3 hydroxyacyl CoA dehydrogenase) reflecting its high dependence on anaerobic metabolism for 400 m racing. The thoroughbred and Arab had the highest activities of aerobic enzymes when compared with the other breeds and in general the donkey had the lowest activities for all enzymes examined and the lowest concentrations of glycogen (Snow and Guy 1981). Within a breed (the thoroughbred) it is also possible to identify animals more suited to sprinting (1000–1600 m) or staying (2400 m–7000 m), the percentages of slow twitch fibres being significantly higher in the staying than the sprinting group (Snow and Guy 1981).

These observations were obtained in animals which had not undergone any recent training. However, training of the animal is associated with some adaptation of fibre types. Along with maturation, training effects a transformation of some Type IIB fibres to highly oxidative Type IIA fibres (Lindholm and Piehl 1974; Guy and Snow 1977; Essen et al. 1980; Henckel 1983) so that fast twitch fibres may by adaptation develop good endurance qualities whilst retaining their high speed of contraction. No effect of training on slow twitch fibres has been observed. Training at submaximal levels also produces increases in the activities of muscle enzymes involved in oxidative metabolism (Snow and Guy 1979; Essen et al. 1980; Henckel 1983). In humans these increases are accompanied by a greater oxidation of fats and a reduced rate of glycogen depletion and lactate production by working muscle during submaximal exercise (Gollnick and Saltin 1982). In the horse, training also has a glycogen sparing effect (Lindholm and Piehl 1974). The animal's ability to utilise NEFAs and spare glycogen at least partly accounts for the varying degrees of glycogen depletion of equine skeletal muscle observed during prolonged exercise although severity of exercise will also have an effect (e.g. Hodgson et al. 1985). Snow et al. (1981) in a study of horses participating in an 80-km endurance race found varying degrees of depletion with a mean utilisation of approximately 60% of pre-ride glycogen concentrations. However, in a controlled study of horses examined at a constant speed (16–18 km/hr) Snow et al. (1982) found complete depletion in some thoroughbreds exercised for distances up to 80 km. Lindholm et al. (1974) observed considerably less glycogen depletion in standardbreds working at a similar speed over a slightly shorter distance.

Depletion usually occurs in Type I and Type IIA fibres first with the Type IIB fibres only being recruited in the latter stages (e.g. Snow et al. 1982; Hodgson et al. 1985). The pattern of depletion is the reverse of depletion and can be a slow process with none of the fibres being repleted 4 hours after exercise and only some being repleted after 24 hours (Snow et al. 1982).

**Muscle Fatigue**

McMiken (1983) suggested fatigue is not caused by a single factor but is the result of various occur-
Physiological Measurements and Their Application to Draught Animals

Measurements of physiological changes fall into two categories: (1) those suited to laboratory conditions, and (2) those that can be applied in the field. Draught animals are often working in hot, dusty, wet or muddy conditions and any equipment used to take physiological measurements under these conditions, all of which might be experienced in a single working day, needs to be robust and reliable. Laboratory studies, making use of treadmills, enable physiological changes to be observed in animals exercised under controlled conditions. These are necessary if physiological changes associated with work in draught animals are to be more completely understood. Cardiovascular and respiratory studies are more suited to a laboratory, whereas studies of blood and muscle parameters, although requiring fairly sophisticated analytical techniques often require larger numbers of animals than can be easily maintained in a laboratory. Measurements such as heart rate, respiration rate and body temperature are relatively easily measured in animals in the field, however, they do not provide a great deal of information. They can, however, be useful in comparative studies, e.g. heat tolerance of crossbred and purebred cattle. Clearly there is a need to look carefully at which measurements can be made in the field and which in the laboratory. The aim of any physiological study of draught animals is to be to knit together observations made in the laboratory with field experiences so that a complete picture can be built up.

References


