

Chapter 1: General Introduction

Generally, draught animal power (DAP) provided by cattle, buffaloes, camels, donkeys and horses is suited to smallholders as it is often difficult for small and marginal farmers to use tractors and other heavy machinery (SLINGERLAND, 1989). Many developing countries in Asia and Africa still depend on DAP for agricultural operations and rural transport (PETHERAM, *et al.*, 1985 and GOE, 1989). For a variety of reasons, these countries will continue to depend on DAP for many years to come (NAGPAUL *et al.*, 1985). In Bali (Indonesia) for example, Bali-cattle, buffaloes and horses are used for DAP. Bali-cattle are usually used for ploughing; buffaloes for both ploughing and carting, and horses for carting only.

In the world at large, the uses of DAP vary from one country to another. For example, in Ethiopia (Africa) farmers employ oxen for cultural reasons and because they are stronger than females and both bulls and bullocks (ANDERSON, 1985). In India, on hilly terrain, and when fields are water logged or affected by rabbit burrows, bullocks are the only available economical source of power (AGARWAL, *et al.*, 1989). Indonesian farmers, on the other hand, use mainly females (cattle and buffalo) as draught animals (DAs), while in China, DAP is based on both male and female cattle (RAMASWAMY, 1985; QIANG, 1985). In Bangladesh, by way of contrast, use is made of males and females of both cattle and buffalo (TAREQUE, 1985).

In the author's home region, Bali, both cattle (the Bali-cattle or *Bos javanicus*) and swamp buffalo are used for DAP, and for both species farmers use mainly the female (75% of use compared to 25% of males). Traditionally, males were used after castration (oxen) in larger numbers, but since the early 1980's the preference of farmers has swung (due to alternate markets becoming available for males for export) almost completely to the use of bulls for DAP; these bulls are then sold for export at 2-3 years of age. Bulls are known to be stronger than cows (SULAEMAN *et al.*, 1989), but farmer observations in Bali indicate that bulls suffer higher levels of heat stress during work, a phenomenon

which limits their work capacity. Little is known of the extent or causes of sex differences in the heat stress experienced during exercise, though MURRAY and YEATES (1967) demonstrated that males were more stressed than females when walking under sunny conditions.

On Bali there are two distinct climatic seasons: the "rainy season" from November until March (classified as "cool/humid"), and the "dry season" from April until October (classified as "hot/dry"). Farmers normally produce 2 crops per year, mainly rice in the rainy season and a mixture of corn, soybeans, peanuts and tobacco in the dry season. As a consequence, DA's are used year round, and under very different climatic conditions. During the cool, humid, rainy season, the evaporation of moisture (from skin or respiratory tract) could be expected to be impeded. This is particularly so for sweat since it is not subjected to the forced air movement experienced during panting. Cattle are well known to rely primarily on sweating as a cooling mechanism (FINDLAY and YANGE, 1950), while buffalo sweat little (FINDLAY, 1950) and thus rely on panting, supplemented by wallowing when available. It seemed possible, therefore, that a season x species interaction could exist between cattle and buffalo, and that this could determine the optimum use of these two species for DAP.

Amongst the swamp buffalo used for DAP in Bali, about 20% are white coat, while the remaining 80% are the normal black colour. Farmers believe the black to be stronger than the white coat, but from a knowledge of the thermoregulatory advantages of a white hair coat to cattle (eg. RIEMERSCHMID and ELDER, 1945; DOWLING, 1960) it seemed possible that white coat animals might in fact be less stressed than black ones during the hot and sunny "dry" season. No data are yet available on this point.

The plan adopted for this thesis was to undertake field trials in Bali under practical farm conditions, and to then conduct detailed experiments in climate rooms at the University of New England, Australia. In Bali, the details of field work were constrained by the "subak" traditions which control husbandry and management practices under both irrigated (rainy season) and dryland (dry season) farming. Under "subak", for example, the yoked together (for DAP) of animals of different species is not permitted.

For this reason, the field work involving ploughing (the major use for DAP), was undertaken with cattle alone in one village, and with buffalo alone in a different, but close-by and climatically identical, village. "Subak" does not apply to off-farm activities such as ground levelling for building construction, and the opportunity was thus taken to compare the physiological responses of cattle and buffalo yoked together under these conditions. Such data are not yet available, although buffalo were found to be stronger than cattle by BAKRIE *et al.*, 1989b. However, as buffalo sweat less than cattle, they are less likely to suffer more from heat stress, particularly during the "hot/dry" season. In practice, buffalo need to be allowed to wallow before and at intervals during work (PIETERSEN and FFOULKES, 1988), or to be periodically doused with water or covered with wet sacking. In Australia, where the detailed climatic work was conducted, neither *Bos javanicus* nor swamp buffalo were available to the author. The decision was thus made to conduct this aspect of the work using goats as an experimental animal. Goats, cattle and buffalo share a hairy pelage, and goats lie between cattle and buffalo in their ability to sweat (ROBERTSHAW, 1968).

The work reported in this thesis thus falls into three distinct areas, all interrelated:

1. Field trials comparing (separately, because of "subak") males and females of both cattle and buffalo pulling the plough under normal farm conditions in Bali. To examine the possibility of a season x species interaction, trials were conducted during both the "rainy" and "dry" seasons in adjacent villages (same soil and climatic conditions) which employed similar feeding and management regimes.
2. Field trials under non-farm village conditions, with female buffalo and cattle yoked together and pulling land-levelling machines (non-"subak") in both the climatic seasons.

3. Climate-room studies in Australia with goats exercised under controlled conditions, in which a number of possible factors associated with the development of heat stress during exercise were studied:

- a. Live Weight
- b. Body Condition
- c. Feed Intake
- d. Breed
- e. Sex
- f. Temperature Levels

In addition, estimates were made of the cutaneous and respiratory moisture losses from various classes of goats, and the effects of physically blocking these two avenues of heat loss (by applying a plastic coat and by increasing the humidity of inspired air respectively) were examined. Finally, the effects of sprinkling water on goats, to simulate a higher sweating rate, were examined with a view to investigating the possible advantages of the customary practice, amongst farmers, of wetting working buffalo, and to establish a theoretical case for the subsequent selection of working animals with enhanced (natural) sweating capacity.

From the foregoing it is apparent that this thesis will focus on the development of heat stress, and on the "heat loss" side of the animal's energy balance equation. Heat production is equally as important, but facilities to measure it satisfactorily were not available to this author. Nevertheless, this area will be covered in detail in the Literature Review which follows, along with the topics bearing directly on the experimental observations made. Throughout this thesis reference to "buffalo" is taken to mean "swamp buffalo" unless otherwise stated.

Chapter 2:

Literature Review

2.1. General

Amongst farm animals, numerous experiments have been reported on the effects of several thermal stressors, including ambient temperature, relative humidity, solar and infra-red radiation, and wind velocity (see, for example, FINDLAY, 1950; DOWLING, 1960; AMAKIRI and FUNSHO, 1980; and BAKER, 1989). After some early field reports (e.g. BONSMAN, 1940a), most of this work was conducted between 1950 and 1970 under indoor, climate chamber conditions. Subsequently, more emphasis has been placed on trials under field conditions (VERCOE, 1969; BROWN, 1971; JENKINSON and ROBERTSHAW, 1971; and DMIT'EL, *et al.*, 1979). It is now recognised (VERCOE, 1969) that not only does "heat stress" result from a variable complex of temperature, humidity, air movement and radiant heat load, but "heat stress" from such causes is only one aspect of an animal's response to its total environment. Disease and nutrition are two additional stressors that are commonly encountered, and the animal's response is also modified by its productive state. Growth, lactation and pregnancy are three productive states that have received experimental attention, particularly in temperate regions.

In contrast, exercise, as exemplified by the use of animals for draught power, a common use of animals throughout the tropics, has received relatively less attention. Numerous field studies on the use of various classes of animals for draught purposes (ploughing, pulling carts etc) have been reported (eg. OLI, 1985; NAGPAUL *et al.*, 1985; and PEARSON and ARCHIBALD, 1989) but relatively less has been done on physiological responses, and less still on factors affecting them. Sex and breed are two factors that have been identified as being associated with different responses during exercise, and many authors agree that environmental temperature and exercise increase respiration rate (RR), rectal temperature (RT), and skin temperature (ST). Changes in evaporative cooling, and its partitioning between the respiratory and cutaneous routes are, however, largely unknown, as are the causes which underlie the observed sex and breed

differences in work potential. The review which follows explores the available evidence in these areas, and the subsequent experiments were designed to examine the various hypotheses developed.

2.2. The Effect of Exercise on Physiological Responses in the Different Sexes

Several experiments on responses to exercise in the various sexes have been undertaken by SYMINGTON (1960a), MURRAY and YEATES (1967) and OHNO *et al.* (1993). MURRAY and YEATES (1967) reported on walking trials with male and female cattle under the sun at 25 to 32°C environmental temperature, and showed that when unclipped animals walked at 4.3 km/h, males (bulls and steers) displayed higher RT of 40.7°C and 40.6°C compared to females (heifers) of 40.1°C. Moreover, at a slower speed (2.7 km/h), bulls and steers again showed higher RT (40.3 and 39.9°C respectively) than heifers (39.6°C). On the other hand, MURRAY and YEATES also reported that when the same individuals had their hair coats clipped and walked at 4.3 km/h, the bulls displayed the greatest increase in RT of 1.9°C (from 38.7 to 40.6°C), followed by steers and heifers with increases of 1.4 and 1.2°C respectively after 4 hours walking. MURRAY and YEATES (1967) reported that RR in heifers was lower during exercise (146/minute) than it was in either steers (172/minute) or bulls (152/minute). Similar patterns of response were observed at 4.3 and 2.7 km/h. With regards ST, values for heifers (37.1°C) were lower than for steers (37.6°C); while at 2.7 km/h the ST of all three sex types progressively decreased by from 1.9 to 2.3°C, with the steers generally displaying the highest to ST of 38.8°C; heifers were lowest at 37.4°C.

In sheep, SYMINGTON (196(b)) demonstrated that young rams (< 1 year) were more capable of maintaining normal RT during exercise at an air temperature of approximately 24°C than older (> 2 years) animals which also had greater live weight. For example, in Persian Blackhead rams, RT changes were +0.8 and +0.9°C and those in RR were +51 and +58/minute in young and mature and young animals respectively during exercise from 7.00 to 11.30 a.m. The ability of young rams to better withstand exercise than mature rams is possibly due to their leggy conformation, their low live

weight and the physical fitness associated with youth, or a combination of all three. LYNCH (pers. comm) reported from experiments conducted in 1966, that under hot, dry conditions in Western NSW, rams walked much shorter distances each day than did ewes.

From the above results it could be suggested that a relatively poor walking performance of males may be one possibility, as well as a greater heat production associated with walking. Moreover, males have a longer mean stride distance in comparison to females (MURRAY and YEATES, 1967), and the greater responses in males may have resulted from a greater mass of muscle involved in locomotion in males than in females. For instance, the bulls studied by MURRAY and YEATES (1967), were approximately 40 kg heavier than either the steers or the heifers, despite being the same age. The sex differences observed in that work are thus confounded by differences in live weight, and possibly body composition. That responses to exercise vary with live weight has been suggested by PEARSON (1939), who reported that when buffaloes carried loads for 6 h/d for a distance of 16 to 17 km at environmental temperatures of 24 to 37°C, RT in both small (237 to 320 kg) and large (401 to 464 kg) individuals increased by about 3.5°C to 41.5 and 42°C respectively. Under the same conditions, cattle showed less than a 1°C increase in RT during the working day and the final values reached were 39.8 and 39.9°C respectively for small (360 to 424 kg) and large (551 to 557 kg) animals.

From this limited evidence, it could be concluded that heavier animals react more than lighter ones during exercise, but the extent to which differences in live weight can explain differences between the sexes remains unclear.

2.3. The Effects of Exercise on Physiological Responses of Different Breeds

ARRUDA and PANT (1984) reported no significant differences in the RT responses of Caninde, Anglo Nubian (AN) and Bhuj goats and Brazilian Woolless and Santa Ines sheep kept at temperatures of 32-35°C and RH of 36-38% prior to or immediately after exercise for 15 minutes. However, the fact that Bhuj and Caninde goats recovered normal RT within 30-45 minutes compared to more than 60 minutes for AN

goats and the woolless sheep ($P < 0.05$), could be due to the Bhuj and Caninde breeds having significantly higher RR (and hence presumably heat dissipation) following exercise than the AN and woolless sheep ($P < 0.05$).

In cattle, the effects of environment on RT and RR are well known to differ with breed. For example, RHOAD (1938) reported that RT and RR of Aberdeen Angus were more affected than those of Zebu cattle by high atmospheric temperature. In addition, RHOAD found that half-bred animals showed superior heat tolerance to three-quarter-bred ones. In support of this, BONSMAN (1940a, 1940b) concluded that Afrikaner cattle were less affected (in RT and RR) than European breeds by a rise in atmospheric temperature. Among the European breeds studied by BONSMAN, the Aberdeen Angus was affected much more than the Hereford. Subsequently, in an experiment on the effects of environmental temperature of different breeds, BADRELDIN *et al.* (1951) showed that the Shorthorn maintained higher levels of RT and RR (38.6°C ; 34/minute respectively) than Jersey and native cattle (38.2°C ; 30/minute, and 38.2°C ; 29/minute respectively). The fact that Shorthorns were more affected physiologically might have been due to their larger size, furry long-haired coats and/or thin, light skin. Such characters are responsible for the failure of the pure and high grades of Shorthorn, for example, to eliminate surplus heat through the skin and as a consequence the animals are forced to increase RT and RR (BRODY, 1945; RIEMERSCHMID and ELDER, 1945; PARER, 1963; THWAITES, 1965, 1967). In the case of the less-affected Jersey, a smaller size and lighter coat colour would have been an advantage. Small animals have a relatively larger surface area than large animals, and this helps in the elimination of heat by radiation, conduction, convection and evaporation (BRODY, 1945).

According to SARAVANAKUMAR and THIAGARAJAN (1992), differences in heat tolerance between Murah, Surti and non-descript buffaloes might be due to differences in sweat gland numbers or in other skin characters. For example, while Murah buffaloes recorded the lowest heat tolerance coefficient (74.5 compared to 76.9 and 80.5 respectively for Surti and non-descripts), their respective skin thicknesses were 8.1, 8.9 and 8.7 mm, and their epidermal thicknesses were 144, 118 and 144 μm . While mean

sweat gland densities of 254, 164 and 224/cm² were recorded in Murah, Surti and non-descript respectively ($P < 0.05$), a comparison of length, diameter, volume and surface area of the sweat glands indicated a less efficient type of gland in the Surti breed.

A comparison of the responses of different breeds of cattle to exercise by YEATES and MURRAY (1966) revealed mean RT increases when walking at 2.7 km/h of 0.4°C in Herefords and 0.1°C in Santa Gertrudis. Corresponding values when walking at 4.3 km/h were 1.0°C and 0.5°C. The steepest increases in RT occurred during the first hour of exercise, and were very obvious at 4.3 km/h; being (38.6 to 39.3°C) and (38.6 to 39.0°C) in Herefords and Santa Gertrudis respectively. The highest RT of 39.6°C was recorded in Herefords in the third hour, and 39.1°C in Santa Gertrudis in the fourth hour, both at 4.3 km/h. Similar patterns were also found in $\frac{3}{4}$ Santa Gertrudis, $\frac{1}{4}$ Santa Gertrudis and Hereford by MURRAY (1966), and in Zebu and crossbred cattle by BUVANENDRAN *et al.* (1992).

Under field conditions, without exercise, TURNER (1982) reported that mean RT differed significantly between breeds. In that work Africander and Brahman had the lowest RT (39.2 and 39.3°C respectively) and Hereford x Shorthorn the highest (39.8°C), with Africander x Brahman intermediate (39.5°C), when environmental temperature varied from 11 to 32°C. TURNER estimated the heritability of RT to be 0.33; other estimates of the heritability of RT in cattle are 0.50 to 0.64 (GARCIA and RODRIGUEZ, 1976), 0.44 (DA SILVA, 1973), 0.50 (KNAPP and CLARK, 1951), 0.15 to 0.30 (SEATH, 1947) and zero (CARTWRIGHT, 1955). From these results it is apparent that differences in heat tolerance within breeds are attributable to genetic, as well as phenotypic factors.

During slow and fast exercise, YEATES and MURRAY (1966) reported that the RR of Herefords exceeded that of Santa Gertrudis cattle. In different breeds, ACHARYA *et al.* (1979) reported that Holstein x Harijana cattle had higher RR at rest prior to the start of ploughing and carting trials than did indigenous animals (30 ± 0.8 vs 26 ± 1.0 /minute), which they attributed to a higher metabolic rate in the crossbreds. Moreover, after 4 hours of ploughing and carting in the rainy season, RR in crossbreds had risen to 74 ± 4 /min

compared to $61 \pm 4/\text{min}$ in the indigenous breeds. These findings were in general agreement with ANAND and SUNDARESAN (1974) in cattle.

Observations on ST by YEATES and MURRAY (1966) indicated that at both slow and fast walking speeds the Santa Gertrudis was less affected than the Hereford (the difference was consistently 1.7 to 2.3°C). However, without concurrent estimates of sweating rate it is not possible to conclude whether the superiority of the Santa Gertrudis was due to the cooling effect of a higher sweating rate, or to a lower metabolic heat load, or a combination of both.

Overall it can be concluded that the Santa Gertrudis responded less than the Hereford during walking trials. YEATES and MURRAY (1966) advanced a number of possible reasons for those differences. Anatomically, Santa Gertrudis cattle appear to be more adapted to walking than British breeds; they have longer legs in proportion to body size, and therefore a longer stride. Thus YEATES and MURRAY observed that the individuals of either breed which walked with the smallest steps also displayed the greatest increase in RT and RR. The Herefords took smaller steps than the Santa Gertrudis (no data available), and this could partly explain the breed differences in response to exercise. The relative performances of Hereford and Santa Gertrudis animals during the walking trials of YEATES and MURRAY (1966) are in general agreement with the results of BONSMAN (1949), who found Herefords to be consistently inferior in this regard to Africander cattle. In addition, BONSMAN demonstrated that coat type plays a vital role in an animal's ability to maintain RT during exercise in the heat, and that woolly coated Herefords and Shorthorns were markedly inferior to smooth-coated individuals of the same breeds. YEATES and MURRAY reported that two of the Herefords in their trials had relatively woolly coats with average hair lengths 2.2 and 3.5 cm respectively compared to the 0.6 - 1.4 cm which would be expected in Zebu cattle (DOWLING and NAY, 1960; and JOHNSON and WEBSTER, 1967). NELSON and HERBEL (1966) support the above breed differences; they observed that Santa Gertrudis

cows spent almost double the time walking and grazing during daylight hours that did Hereford cows.

Under field conditions in the tropics (ploughing and carting), a number of studies confirm the existence of quite marked breed differences in heat tolerance. Thus observations on Ongole, Bali and Madura cows during exercise at 3 km/h (MA'SUM, *et al.*, 1991) indicated that the Ongole was superior to the Bali and Madura in its ability to sustain a work load. The Ongole was better able to cope with high ambient temperature and humidity, possibly due to its white colour and its Brahman blood, but specific causes were not investigated. The advantages of the Ongole can be seen in lower RR, RT and ST (33, 57, and 42/minute) than in the Bali and Madura breeds (38.4, 38.8, and 38.4°C and 34.3, 35.3 and 35.0°C respectively).

In the work of ACHARYA *et al.* (1979), the ploughing capacity of Holstein x Hariana bullocks was non significantly greater (speed, depth of furrow and area ploughed) than in indigenous types, but both genotypes exhibited better ploughing capacity during winter than in either summer or the rainy season. NAGPAUL *et al.* (1985) reported a superiority of Zebu animals over Jersey crossbreeds. Furthermore, ACHARYA *et al.* (1979) reported that during winter, both types did not show any panting or salivary frothing, indicating that the weather was "comfortable" for work. The manifestation of these physical signs of heat stress in crossbreds could be minimised, and their working efficiency increased, if the animals were worked during the early morning and late evening when the weather was hot (THOMAS and PEARSON, 1986; and BHOSREKAR and MANGURKAR, 1988). Subsequently, in comparisons of cattle with buffaloes, NAGPAUL *et al.* (1985) found that behavioural responses such as panting, dribbling of saliva, tendency to tire and shelter seeking were noted in buffalo bullocks after only 2 hours of work, whereas, Zebu and crossbred bullocks did not exhibit these symptoms even after 4 hours of work. The trends in these findings were confirmed

by AMAKIRI and FUNSHO (1980), working with cattle in Africa, and by KHALIL *et al.* (1990).

2.4. The Effects of Nutritional State on Physiological Responses During Exercise

Much research has been done on nutrition-exercise interactions, and as a general rule it has been concluded that animals on better quality diets produce more heat than those on poorer quality ones, and that glucose as well as acetate are metabolized as energy sources during both rest and exercise. Confirmation of this is provided, for example, by JARRETT *et al.* (1976) who reported that the utilization of glucose was greatly increased by exercise: during work glucose supplied about 27% of the energy for respiration in an exercising limb whereas acetate supplied only about 2%. In complete contrast, in the resting limb little utilization of glucose was recorded although acetate oxidation accounted for about 20% of the oxygen uptake. Concurrently, JUDSON *et al.* (1976) reported that at rest the total entry rate of blood glucose was 0.44 ± 0.03 mmol/min, while during exercise it was 0.84 ± 0.004 mmol/min. Similar patterns were also reported by HARMAN and PETHICK (1994).

At a different physiological level, further information is to be found in the work of CLARK AND QUIN (1947), who reported that when sheep were exposed to environmental temperatures of 9-23°C in the field, thin sheep on a poor diet (600 g/d grass hay) showed a suppressed panting reflex (20-40 vs 90-150/minute) and an excessive rise in RT (37.2-39.3°C vs 38.3-39.5°C) in comparison to those on a better diet (350 g/d maize and 790 g/d lucerne hay). Moreover, the ability to control RT returned when body condition improved. This result was supported by ROBINSON and LEE (1947), who noted that a high-plane diet fed to ewes induced very highly significant increases in RT and RR in both hot-wet and hot-dry atmospheres when compared to a low-plane diet. Subsequently, an experiment using 3 different levels of diet ("low", 300-400 g/d; "medium", 500-850 g/d; and "high", 800-1400 g/d) for Merino and Corriedale ewes (RIEK, *et al.*, 1950) revealed that these sheep were generally relatively tolerant of

hot conditions; the exceptions were the high-plane Corriedales, which had to be removed before the completion of seven hours of exposure to 40°C and 40 mm.Hg water vapour pressure, with a RT over 41.7°C. Subsequently, in cattle PURWANTO *et al.* (1993) reported that both RR and RT at a high level of TDN intake (72.5 g/kg^{0.75} day) were the same as at a medium level (80% of the high level), but both those values were higher ($P < 0.05$) than at a low level (60% of the high level). At all levels of TDN intake, the mean of standing HP (heat production) was higher ($P < 0.05$) than the resting (lying) HP. The differences between standing and lying HP at low, medium and high feeding levels were 4.4, 4.7 and 5.4 kJ/kg^{0.75} h, respectively; values which represent only 7% of total HP. In sheep, GRAHAM *et al.* (1959) found that low (600 g/d), medium (1200 g/d) and high (1800 g/d) levels of feeding in sheep produced heat at rates of 0.23, 0.35 and 0.42 KJ/h respectively when environmental temperature varied from 24 to 40°C. Also in sheep, CLAPPERTON (1964a) reported that the mean apparent digestibilities (%) of dietary constituents (at a submaintenance feeding level) by the Cheviot and Scottish Blackface breeds, when at rest or walking on a treadmill at 2.9 km/h on a gradient of 17° for 260 minutes, were:

Table 2.1 The digestibility of dry matter and heat production in sheep at rest and when walking

Breed	Dry matter digestibility (%)		Heat production (%)	
	rest	walk	rest	walk
Cheviot	65.9±1.5	66.7±1.3	64.4±1.6	65.8±1.9
S.Blackface	64.6±0.8	65.1±1.3	64.0±1.8	64.1±2.2

From a combination of the above results it can be seen that different breeds of sheep have different capabilities to digest foodstuffs, and that in general sheep digest more efficiently as well as produce more heat, when walking than when resting.

In working animals, BAKRIE *et al.* (1989a) reported that buffalo had a significantly higher RT during work when given a roughage diet than when fed a concentrate diet. In addition, while the RT of buffalo on the concentrate diet remained lower at all times during work, RR followed the opposite trend and remained higher on

this diet compared to the roughage diet. This differential responses in RT and RR is not unexpected, since increased evaporative cooling from a high RR would automatically reduce RT. Nevertheless, the use of diets of lower heat increment seems to reduce the heat load in working animals, particularly buffalo. Moreover, BIRD *et al.* (1981) reported that treadmill exercise at 2.5 km/h on a 10 degree slope for 60 min in sheep caused a six- to seven-fold increase in hind-limb oxygen uptake (364 vs 2360 $\mu\text{mol/min}$), due mainly to an increase in blood flow, assisted by an increase in the oxygen-carrying capacity of arterial blood. Subsequently, at rest, the oxygen uptake was 355 and 373 $\mu\text{mol/min}$ when feed was given at maintenance (5.8 MJ/day) and 1.5 times maintenance (8.6 MJ/day) respectively. Meanwhile, during exercise the corresponding oxygen uptake values were 2114 and 2606 $\mu\text{mol/min}$ ($P < 0.05$). Subsequently, RICHTER *et al.* (1992) reported that in the human leg the oxygen uptakes at rest and during 30 minutes exercise were 89 and 4192 $\mu\text{mol/min}$ respectively.

Experiments on exercise in steers fed low and high plane diets (MURRAY *et al.*, 1981) revealed that the RT response to exercise was greater in the high than in the low plane group. For example, after 2 h of exercise the high plane group showed increases in mean RT of 2.1 to 2.2°C compared with values of 1.7 to 1.8°C for the low plane group ($P < 0.05$). Compared with high plane animals, low plane animals also had lower RR before and after 2 h of exercise, although mean values were not significantly different (125 ± 17 vs. 161 ± 4 and 202 ± 6 vs. $219 \pm 11/\text{minute}$ respectively). In addition, high plane animals had significantly greater ($P < 0.05$) sweating rates than low plane animals (474-615 vs 267-332 $\text{g/m}^2/\text{h}$ respectively). The same patterns were reported by SLEE *et al.* (1988) in sheep; after 1h of heat exposure, sheep on unrestricted feeding had slightly higher RT (40.0 ± 0.0 vs $39.6 \pm 0.2^\circ\text{C}$; $P < 0.05$) and much higher RR (138.7 ± 58.4 vs $32.0 \pm 20.0/\text{min}$; $P < 0.05$) than those on restricted feeding.

The values for the energy cost of walking and working in various draught animal species are illustrated by the following (after LAWRENCE and STIBBARDS, 1990):

Table 2.2. Summary of available data on the energy cost of walking in cattle and buffalo

	Average value	Species	Source	Comments
Energy cost of walking (J/m/kg live weight)	1.9	Cattle (Bos taurus)	Brady (1945).	Weights 383 to 430 kg; speeds 1.8 to 3.2 km/h
	2.0	Cattle (Bos taurus)	Ribiero <i>et al.</i> (1977)	Speeds 2.5 to 5.0 km/h
	0.5 to 2.8	Cattle (Bos taurus)	King (1981)	200 kg animals fed at maintenance; speeds 1.4 to 5.8 km/h
	2.1	Brahman cattle/ buffaloes	Lawrence and Stibbards (1990)	Speeds 1.4 to 5.8 km/h

2.5. The Effects of Exercise on Heat Production

Generally, animals need energy for the maintenance of body functions and activities, particularly when they are walking or exercising (TAYLOR *et al.*, 1974; BORUT *et al.*, 1979; and LAWRENCE and STIBBARDS, 1990) and this is considered as heat production. The energy is mainly derived from carbohydrate oxidation via pathways described by the general formula $C_6H_{12}O_6 + O_2 \rightarrow CO_2 + H_2O + \text{energy}$. In sheep, HARMAN and PETHICK (1974) reported that the contribution of glucose to whole body CO_2 production was low in animals at rest, with values in close agreement with previous work (WILSON *et al.* 1983, ODDY *et al.*, 1985). However, during exercise oxidation increased dramatically, with the absolute rate of glucose oxidation increasing by about 5- and 9-fold when walking below and above the anaerobic threshold respectively. This work confirms that glucose is an important aerobic energy source during physical work. In addition, heavier animals have been shown to use more energy for walking than lighter ones (KING, 1981) and there is a general tendency for energy utilization to increase with increases in walking speed (LAWRENCE and STIBBARDS,

1990) according to the general equation for all animals of: $E_w = 0.974V + 1.199$ (E_w =Joules above standing/m/kg live weight; V =speed m/s).

In running gazelle, TAYLOR *et al.* (1974) described heat balance as: heat production = heat storage \pm total evaporative heat loss \pm non evaporative heat loss, and noted that heat production increased linearly with increasing running speed. For example, at a speed of 3 km/h, heat production was 1.8 times the observed resting levels, and this increased to 8.4 times at 21 km/h (14.9 times predicted standard metabolic rate). Heat storage increased by 32, 74 and 77% as treadmill speed increased to 9.6, 15.8 and 20.2 km/h respectively. While evaporative heat loss increased over 6-fold as running speed increased from 0 to 9.6 km/h, nonevaporative losses declined as treadmill speed increased to 3 and 9.6 km/h (by 50 and 24% respectively). Therefore, most heat loss was through evaporation, particularly by panting rather than sweating since the latter did not increase significantly and remained at approximately 30 g/m²/h. TAYLOR *et al.* concluded that exercise would not have a major effect on the water balance of gazelles due to the fact that they normally either move slowly when they graze or sprint for only short periods to avoid predators.

In comparing different species, TAYLOR and ROWNTREE (1973) reported that goats appear to be intermediate between the "regulator" and "heat storer" classes of animal, in that they store about 35% of heat production; compared to the cheetah and rhea in which 65 and 20% respectively of heat production were stored during 15-30 min on a treadmill at 9 km/h and 22°C. In addition, there were two important differences in the heat balance between cheetahs and goats that were running. Firstly, heat storage was much more important in the cheetah than in the goat. Secondly, neither evaporative nor nonevaporative heat loss of the cheetah increased with increasing heat production, whereas both increased in the goat. For example, as the cheetah increased speed from 2 to 11 km/h, heat storage increased from 5.0 to 31.4 KJ/kg/h, and about 70% of the heat produced while running at 11 km/h was stored. In contrast, total evaporation increased only from 6.2 to 10.5 KJ/kg/h, and only 24% of the heat produced at 11 km/h was lost by evaporation. Nonevaporative heat loss from the cheetah actually decreased (from 5.9 to

2.8 KJ/kg/h) and accounted for only 6% of the heat produced at 11 km/h. A quite different heat balance occurred in goats. As speed increased from 1 to 9 km/h, heat storage increased from 0.2 to 12.6 K./kg/h, but accounted for only 34% of the heat produced at 9 km/h. Evaporation from goats increased nearly 10-fold (from 1.8 to 17.0 KJ/kg/h) and 43% of the heat produced at 9 km/h was lost by evaporation, while nonevaporative heat loss also increased (from 6.8 to 10.3 KJ/kg/h) and accounted for about 26% of heat produced at the same speed. In conclusion, it can be said that the cheetah has not developed evaporative cooling mechanisms for maintaining a constant body temperature during running and instead stores heat, while goats have developed the opposite strategy.

Subsequently, in goats, BORUT *et al.* (1979) reported that while under mild conditions, in the morning at 26°C, evaporation accounted for up to 50% of the heat produced, at 40°C in a climatic chamber it equaled heat production, and at 12.00h in the desert it had increased to about 150% of heat production. In the climatic chamber the goats relied mainly on panting to dissipate heat. In the desert, however, the amount of heat dissipated by sweating was twice as great as that lost through the respiratory system. These high rates of sweating (up to 143 g/m²/h) were attributed to increases in ST consequent on the absorption of solar radiation, a factor which does not exist in the laboratory but is very prominent in the desert environment. Unfortunately, BORUT *et al.* did not compare the different sexes. In a separate experiment comparing buffalo and cattle (Zebu and Hereford), TAYLOR *et al.* (1970) reported that cutaneous water losses from buffalo, Zebu and Hereford animals corresponded to 4.1, 4.3 and 4.7 % of their body weight or 58, 69 and 61% of total water losses, when water was given by free access at 22-40°C environmental temperature in the African desert. The remaining water was lost in the faeces and urine. When water intake was restricted, evaporation was reduced by an amount equal to or greater than the combined reduction of faeces and urine in cattle (300%), but less in buffalo (60%). Thus evaporation was clearly the major avenue of water loss from bovids under desert conditions, and the fact that the buffalo had the largest water loss could be due to it being a poor sweater.

Similar patterns were found by TAYLOR and LYMAN (1972) in two different types of gazelle: the Thomson gazelle stored large amounts of heat while running which led to an increase in RT of as much as 4.6°C, but their corresponding increase in sweating was relatively low (56 vs 78 g/m²/h before and after running respectively). Under the same conditions, Eland increased RT only slightly (less than 1°C), but experienced an increase in sweating of from 96 to 266 g/m²/h.

Overall, it can be concluded that animals of different breeds and species have different ways to maintain heat balance, and that these vary to a considerable degree with body size, environmental conditions and sweat gland output.

In general, a ruminant needs energy for any of the purposes of maintenance, pregnancy, growth, fattening, lactation and work and these are known as net energy requirements, because an animal has to expend energy on the nutrients it absorbs in order to use them for any such processes (LAWRENCE and STIBBARDS, 1990). While, the ARC (1980) stated the standard energy requirement for horizontal locomotion to be 1.2 MJ/km for a 600 kg cow, the corresponding figure according to TAYLOR *et al.* (1989) is 1.0 MJ/km and TAYLOR *et al.* (1970) concluded that the energy cost of running is related to body weight. Subsequently, TAYLOR (1974) reported that a 400-kg ox, walking at a speed of 2 km/h could be expected to expend an amount of energy 11% higher than its resting metabolic rate. Moreover, experiments on the heat production of calves of different body weights kept out-of-doors (HOLMES *et al.*, 1976) suggested that heat production increased (6.2 vs 6.5 kJ/kg/h) with increasing body weight (94 vs 122 kg respectively). RIBEIRO *et al.* (1977) reported that the rates of heat production of cattle walking on a treadmill on the level and at a gradient of 6° were 2 and 26 J/kg/m respectively. Values (J/kg/m) for other species during horizontal locomotion are: man 2.3 (HALL and BRODY, 1934); dog, 2.5 (LUSK, 1931); horse, 1.6 (HALL and BRODY, 1934); sheep, 2.3 (CLAPPERTON, 1964b) and red deer 2.6 (BROCKWAY *et al.*, 1965) and it appears that between these species the energy cost of moving 1 kg of body horizontally is fairly constant.

LENG (1985) concluded that the total daily heat production of a tethered animal is 1.5 times higher than its basal metabolism; in an animal walking with a companion when ploughing the increase is to 2.0 times its basal metabolism whereas an animal actually ploughing increases its daily heat production by 3.8 times its basal metabolic rate. Other factors such as temperature levels are also known to affect dairy heifers (PURWANTO *et al.*, 1994); heat production at 20°C was almost the same as at 10°C, but that at 30°C was 11% higher than at 10°C; such an increase could partly be associated with the high energy cost of standing (CLAPPERTON, 1964b), since animals at 30°C stood for 104 min/d longer than those at 10°C. PURWANTO *et al.* (1994) estimated the energy cost of this additional standing to be 9.2 kJ/kg^{0.75}d, as compared to about 64.8 kJ/kg^{0.75}d as a result of increased metabolic and thermoregulatory activities associated with the concurrent 1.3°C rise in RT. With regards different altitudes, HAYS *et al.* (1978) pointed out that exercise effects in oxen were greater at 3500 m than at 400 m (in heart rate, RR, Hb, blood pH, blood lactate and blood pyruvate by 26, 11, 4, 0.3, 39 and 56% respectively) and suggested that energy expenditure was greater at high than low altitude.

YAMAMOTO (1989a, 1989b) observed that in cattle the levels and daily fluctuations in heat production were closely related to feed intake and feeding time. For example, heat production decreased gradually by 40, 39, 35 and 28 kJ/kg^{0.75}h, when level of TDN intake declined from 15.5 to 14.2, 11.0 and 8.8 kg/day respectively. Such a finding was supported by MATSUMOTO *et al.* (1990), who reported that calves at 100 kg body weight with feeding levels of 100, 85, 70 and 55% TDN produced heat at rates of about 40, 33, 30 and 27 kJ/kg^{0.75}/h respectively. Additionally, it was found that heat production declined with increasing body weight. For example, cows weighing 330 kg and fed similar TDN levels produced heat at rates of 33, 32, 29 and 26 kJ/kg^{0.75}/h respectively.

In working buffalo and cattle (3.6 km/h treadmill speed, 13-20°C environmental temperature and 47% relative humidity) PEARSON and SMITH (1994) reported that heat production was 0.1 and 0.2 kJ/kg^{0.75}/h when dry matter intakes were 2.6 and 3.2

g/kgM^{0.75}/h respectively and feeding time was restricted (food troughs were removed at 08.30h and replaced at 15.30h). However, daily exercise (0.5-3 km/day) did not significantly affect voluntary dry matter intake and heat production in dairy cows (GUSTAFSON *et al.*, 1993). It is assumed that different levels of heat production are closely associated with different levels of oxygen consumption during exercise. For example, in exercising goats, FUKURA *et al.* (1986) observed an increase in oxygen consumption from 0.7 l/kg^{0.75}/h when resting to 1.1 and 1.4 l/kg^{0.75}/h when walking at 1.5 or 3.7 km/h. In exercising sheep, (2.6 km/h) BELL *et al.* (1983) suggested that oxygen consumption increased by 4.5-fold in the thermoneutral zone (14-17°C), a response that was slightly higher than at 23 to 40°C (4.3-fold). The sheep at 40°C relied particularly on panting (RR increased from 84 to 134/min) as the major avenue of heat loss, a condition supported by the finding that blood flows to the nasal mucosa and turbinates of the upper respiratory tract increased about 12- and 30-fold respectively. Subsequently, PETHICK *et al.* (1991) observed increases in the oxygen consumption of both the gut and liver of sheep as treadmill speed and inclination were increased.

The heat production of cattle and buffalo during walking, carrying and pulling increased from 2.1 to 4.2 KJ/km/kg live weight as speed increased from 1.4 to 5.8 km/h; and the animals became visibly uncomfortable (LAWRENCE and STIBBARDS, 1990). Those results were in general agreement with HALES and FINDLAY (1968), who concluded that the oxygen consumption of cattle increased during exposure to severe heat.

Overall, it can be concluded that the major factors likely to affect heat production in domestic animals during exercise (including work load) are body weight, speed, the gradients attempted, feed intake, ambient conditions (including temperature and solar radiation) and altitude. The increases have important practical outcomes, in that they clearly indicate the need for greater feed intake in working animals. However, as indicated in the "General Introduction", the research work undertaken in this thesis

concentrated on the heat loss side of the heat balance equation, and issues of heat production will thus be considered further only by way of discussion of the results obtained.

2.6. The Effects of Exercise on Evaporative Water Loss

Quite extensive studies have been reported on losses of moisture through sweating and respiratory activity in a number of domestic species, but to date the effects of exercise, a potent thermal stimulus, have been largely overlooked.

Sweat glands and sweating:

Differences in sweat gland size have been demonstrated between breeds and strains of cattle (NAY and DOWLING, 1957; NAY and HAYMAN 1963; PAN 1963); the conclusion being that those which are better able to control body temperature in the heat have the largest glands. In addition, heat tolerant animals such as Zebu cattle and their crosses have higher follicle densities than less tolerant European-breed animals (NAY and HAYMAN 1956; TURNER *et al.*, 1962). For example, the mean number of sweat glands per square centimetre on the midside region of Sindhi, Sahiwal, Jersey, Friesian and Red Poll cattle were 1509, 1507, 1005, 996 and 981 respectively. NAY and HAYMAN (1956) also reported that Zebus had much larger (longer and greater diameter) sweat glands than European cattle.

The above results were extended by TANEJA (1959a), who reported a significantly higher rate of cutaneous evaporation from the shoulder of Zebu cross cattle (230.3 ± 37.9) than from Shorthorn (54.9 ± 5.1 g/m²/h). In those same animals, the Zebu cross had lower skin temperatures (36.3 to 39.0°C) than Shorthorns (36.3 to 39.5°C), as might be expected from their higher sweating rates. In another experiment, with Shorthorns, TANEJA (1959b) observed that an increase in skin temperature of from 37.6 to 39.8°C after exposure to high temperature was followed by a progressive increase in cutaneous evaporation of from 214.9 to 422.5 g/m²/h. The corresponding increase in Zebu crosses was from 229.6 to 377.2 g/m²/h, associated with an increase in skin temperature of only 1.7°C. TANEJA also observed that sweating rate was proportional to

the difference between the water-vapour pressure at skin level and that in the adjacent air: differences in vapour pressure of from 11 to 18 mm. Hg. were associated with increases in cutaneous water loss of from 214 to 398 g/m²/h.

Another factor shown to influence sweating is season (SCHLEGER and TURNER, 1965); maximum sweating rates were significantly lower in winter (307 ± 18 g/m²/hr) than in summer (494 ± 6 g/m²/hr) when measurements were taken outside at mean environmental temperatures of 21.7 and 36.7°C respectively. It would appear that temperature and solar radiation contribute substantially to that seasonal effect, though no direct testing of that possibility has been undertaken.

According to SCHLEGER and BEAN (1971), the density of dermal arteries and the percentage of active follicles are the two skin characters most closely related to sweating performance in cattle. They associated sweating rates on the shoulder of different animals of 648 g/m²/h and 191 g/m²/h with 22 and 10 dermal arteries/cm², with 17 and 13 upper dermal nerves/mm², and with 20 and 15% of active follicles respectively. They also found differences between positions on the one animal. In one case, for example, the shoulder and flank had sweating rates of 648 g/m²/h vs 601 g/m²/h and had 22 and 10 dermal arteries/cm² respectively.

Study of buffaloes (DOLLAH and ROBERTSHAW, 1989) revealed that part of the individual variation in heat tolerance could be accounted for by differences in sweating function. For example, tolerant buffaloes sweated at 83-96 g/m²/h, while intolerant animals (body temperature 1°C higher) sweated at only 49-54 g/m²/h. The same authors concluded there was no relationship between skin colour (albino or black) and sweating rate, and that sweating rate could thus be used as a single selection criterion for ability to withstand a heat load.

The body areas with the highest rates of sweating in Ayrshire calves at 35-40°C were fore-quarter trunk (180 % of the mean level from the dewlap, thorax, mid-flank and mid belly) and the neck (140 %; McLEAN, 1963). McLEAN concluded that at low temperatures, on the other hand, the rate of moisture vaporization was low and similar in all regions. PAN *et al.* (1969) subsequently concluded that in Jersey cattle, sweating rate

appeared to decrease posteriorly and ventrally, except that the shoulder region had a particularly high rate. Furthermore, DMI'EL *et al.* (1979) reported that when exposed to solar radiation the Black Bedouin goat has a mean sweating rate from the thorax of 137 g/m²/h, which is approximately six times greater than that reported by JENKINSON and ROBERTSHAW (1971) for British Saanen goats exposed to an air temperature 40°C. This difference could have been due to the black fur and skin of the Bedouin goat increasing the absorption of shortwave radiation (BORUT *et al.*, 1979). This breed of goat could have evolved a greater sweating capacity than other breeds in order to dissipate the additional summer heat load associated with its colour and geographic location in the semi-arid deserts of the Middle East. Another possible reason for the greater sweating ability of Black Bedouin goats is a higher sweat gland density. JENKINSON and ROBERTSHAW (1971) reported that the mean sweat gland density on the upper thorax of five British Saanen goats was 1.7 glands/mm² with a range of 1.0 to 2.7 glands/mm², whereas in the Black Bedouin goat sweat gland density varied from 1.7 to 2.6 glands/mm² with a mean density of 2.1 glands/mm².

HALES *et al.* (1968) and JENKINSON and ROBERTSHAW (1971) have both calculated the secretion rate of individual sweat glands from the upper thorax of cattle to be between 11 and 16 nl/h, whereas the corresponding rate in Saanen goats was 13 nl/h. In contrast, the mean secretion rate of each gland of the Black Bedouin goat was estimated at 66 nl/h.

NIJLAND and BAKER (1991) observed sweating in goats in an environmental chamber at 45°C and < 30% RH and found it to be episodic, with synchronous gland discharges as in sheep (BLIGH, 1959). Each sweat peak was followed by a reduction in both the temperature of the fur surface, of shaved skin and of the deep dermis below both shaved and furred surfaces. For example, in the ninth minute of exposure, sweating rate rose from 44.3 to 48.5 g/m²/hr, whereas, shaved ST decreased from 42.5 to 40.2°C and deep ST below shaved and fur surfaces declined from 40.1 to 39.3 and from 40.8 to 39.7°C respectively. These findings support earlier studies which indicated that sweating can be an important avenue of heat loss in goats (DMI'EL *et al.*, 1979; BAKER, 1989).

On the other hand, FINCH *et al.* (1982) studied different breeds of cattle (Brahman=B; Brahman x Hereford - Shorthorn cross-breeds=BX; and Shorthorn=S) and reported that high sweating rates were necessary to maintain the RT of grazing animals between 08.00 and 16.00 h. For example, the relationship between sweating rate and RT was greater for B (294 g/m².h/°C) than for S (194 g/m².h/°C) and BX (146 g/m².h/°C). This fact could help to explain why the mean RT in B was lower than in other breeds (38.7, 39.3 and 39.7°C for B, BX and S respectively). These results were in general agreement with those of SCHLEGER and TURNER (1965), who found that Brahman x Shorthorn had higher sweating rates than Shorthorn when grazing at 11.00, 14.00 and 16.00h daily (temperature vary from 22 to 37°C): 406 vs 377, 621 vs 519 and 473 vs 427 g/m²/h respectively. Under these conditions the Brahman crossbreds again showed significantly lower RT (37.2°C) than the Shorthorns (38.9°C).

According to BIANCA and FALES (1970), the age of cattle also affects their sweating rate. Thus the rate of moisture loss from the skin per unit of metabolic body size ($W^{0.75}$) at 46°C temperatures was greater in newborn calves than in those 1-year old (190 vs 165 g/m²/h). From a comparison of the two different ages it was concluded that sweating began when ST was about 37°C, that sweating broke out in newborn calves at a slightly lower ST than in 1-year-olds, and that maximal sweating rates occurred at a lower ST in newborn calves (12.2 g/m²/h when ST 38°C) than in 1-year olds (9.3 g/m²/h at 39°C). Similar patterns have been found in humans (STEPHENSON and KOLKA, 1985 and KOLKA *et al.* 1994).

Respiratory moisture loss (RML):

Exercise reduces heat tolerance, often with lethal consequences in the hotter areas (SMITH, 1961). Moisture can be evaporated from the respiratory tract and the rate increased considerably by panting. In order to calculate heat loss from measurements of respiratory moisture loss (RML) it is usually assumed that the moisture is initially at deep-body temperature, that all the moisture lost is evaporated and that the heat for

vaporization is taken from the body and not the air. The latent heat of vaporization of respiratory moisture is thus the value which has been determined for water (YOUSEF, 1985).

Sheep normally pant and sweat, but panting is the major route of heat loss (ALEXANDER and WILLIAMS, 1962). Considering sheep in more detail, ALEXANDER and WILLIAMS (1962) demonstrated that in lambs a minimum RR of about 40/min was associated with sweating and RML losses each of which were equivalent to about 10 g/m²/h, and that at low humidity both RR and RML increased linearly with increasing environmental temperature above the lower critical temperature. Consequently, RML is approximately proportional to RR, and at low humidity is about 0.25 g/m²/h per respiration, or 1 ml from a lamb for each breath (Fig. 1).

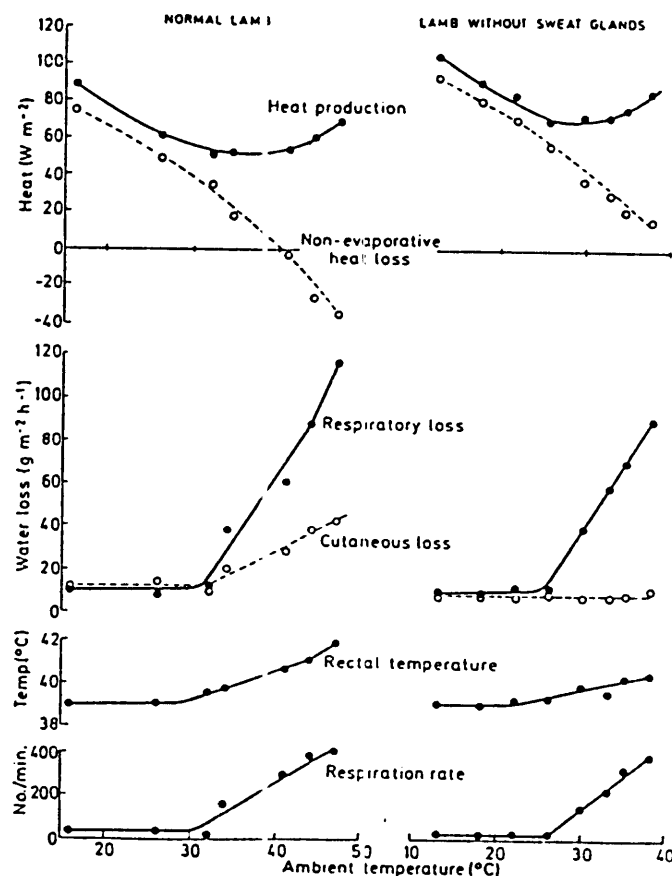


Fig. 1 Thermoregulation in a normal Merino lamb and a Merino lamb without sweat glands from measurements during the first week of life (from ALEXANDER and WILLIAMS, 1962)

ALEXANDER and WILLIAMS concluded that RML increased by from 25 to 110 g/m²/h as RR increased by from 100 to 400/min respectively and that there was a quadratic relationship between RR and RML per respiration; eg. when the RR increased from 100 to 400/min, RML per respiration declined from about 20 to 4 mg/m²/respiration respectively (Fig. 2).

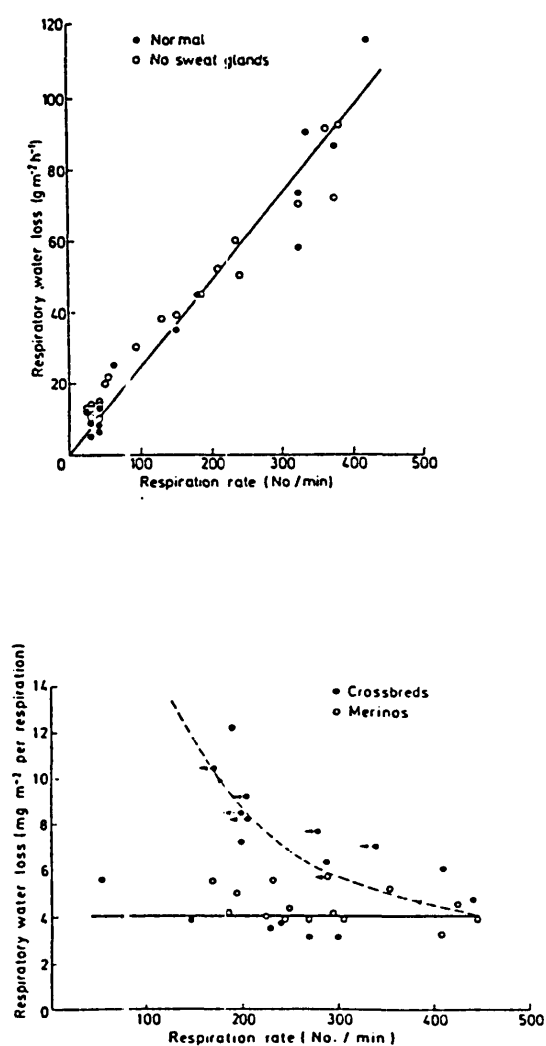


Fig. 2 Relationship between RR, RML and RML per respiration in Merino lambs. The horizontal line represents the RML during normal shallow panting, assuming a constant loss of 4 mg per respiration (from ALEXANDER and WILLIAMS, 1962)

According to BROCKWAY *et al.* (1965), about 20% of total body heat is lost via RML when sheep are in a neutral environmental temperature (12°C and wool depth 10 cm). However, at a higher temperature (35°C) RML increased approximately threefold and accounts for about 60% of total heat loss. In goats, when environmental temperature increased from 10 to 30°C, RML rose from 9 to 20% of total heat production (JESSEN, 1977). McLEAN and CALVERT (1972) reported that at 15°C steers lost 10% of their heat via respiratory evaporation, while at 35°C evaporation from the respiratory tract and the skin both increase, but sweating increases most and respiratory evaporation accounts for only 32% of total heat loss. These results support those of KNAPP and ROBINSON (1954), that at 40°C the RML in Jersey cows averaged 116 g/hour, while the corresponding average loss from Corriedale ewes was only 50 g/hour. The first reaction to heat observed by KNAPP and ROBINSON in both cows and ewes was an increase in RR. This happened within half an hour of entering the hot-room (42°C) by which time the RR of sheep was 240/min and that of cattle was 60/min. Additionally, with both species, ST rose with increased RT; the ST of the cow was 0.8-1.1°C lower than its RT whereas the difference in the sheep was 0.3-0.6°C, a difference which is consistent with greater water evaporation from the skin of the cow than the sheep. Such a suggestion was confirmed by the observation that as temperature increased from 30 to 40°C, sweating loss in the cow increased from 118 to 176 g/m²/h and in sheep from 74 to 95 g/m²/h respectively. It can be concluded that the sheep depends more on respiratory cooling than does the cow. This conclusion was confirmed by KNAPP and ROBINSON (1954), who reported that respiratory water loss in the cow amounted to about one-fifth to one-ninth of its water loss, whereas in the sheep the proportion was about one-third.

2.7. The Effect of Season ('wet' and 'dry') on Physiological Responses During Work

Studies of the effects of different seasons on the physiological responses of cattle and buffalo are rare. In fact the only relevant literature is the experiment of BADRELDIN *et al.* (1951) conducted during winter (November to March) and summer (April to August) in Egypt. Environmental temperature varied from 5 to 26°C and 15 to 36°C

during winter and summer respectively and RH varied correspondingly from 62 to 84%, and from 50 to 65% in summer. BADRELDIN *et al.* found that during winter the animals had lower RR and RT than in summer. The effect of season on RT and RR showed nearly the same trends in both cattle and buffaloes, with cattle always having the higher values.

BADRELDIN *et al.* (1951) concluded that the fact that RT and RR of river buffaloes are lower than in cattle may be considered as a species difference. However, buffaloes seemed to suffer much more from hot weather than cattle, and the relative increase in RT and RR with air temperature was more pronounced in buffaloes than cattle. Such facts were confirmed by LAKRIE *et al.* (1989b, 1989c), who found that RT and RR reached higher levels following one hour of work by buffalo than after 2 hours' work by cattle, but the rate of decline during recovery in the shade was similar in both species. These species differences may be due to the fact that buffaloes possess dark, tough and semi-hairless skin, and as a consequence absorb more heat when exposed to solar radiation; they also sweat little (PHILLIPS, 1948). Since the number of hairs per unit area of skin surface indicates the number of sweat glands in cattle and buffalo (FINDLAY, 1950; FINDLAY and YANGE, 1950), buffalo may also be considered to have fewer sweat glands than cattle. Furthermore, buffaloes are heavily muscle animals and the heat lost from their skin is relatively less than in smaller cattle. The above characters all probably contribute to the discomfort showed by buffaloes during summer.

All the above patterns were supported by the findings of LEE *et al.* (1976) who reported that RR and RT increase markedly (3 fold and 0.8°C respectively) during the hot as compared to the cool seasons in lactating Holstein cows, when mean maximum and minimum ambient temperatures and relative humidities were 33.6, 21.5°C, and 55.5% vs. 20.4, 9.9°C and 97.5% respectively. Observations on buffalo and cattle were also made by PEARSON (1989), at an environmental temperature of 24-37°C for a total of 6 days, with work at a speed of 3.6 km/h. Cattle maintained this speed for most of the day whereas buffaloes showed a steady decrease in speed to 3.2 km/h in the last hour. RT of buffaloes increased during work; by 3.5 h an increase of up to 3.5°C was observed. It was then necessary to stop and let the buffaloes wallow for about 20 min before they would

continue to work. During wallowing, RT decreased to or below values seen at the start of the day. Cattle, in contrast, showed increases of $< 1^{\circ}\text{C}$ in RT during work.

RR in the buffaloes of PEARSON (1989) increased > 2 -fold as they began panting (usually after 1.5-2.5h of work). RR of cattle, on the other hand, increased up to 3-fold during work. It was concluded that buffaloes and cattle have a similar daily work output. Such a conclusion is supported by PIETERSEN and FFOULKES (1989) who showed that wet hessian sacking placed over animals reduced the effect of the climatic variables such as ambient temperature, relative humidity and solar radiation; thermoregulatory responses (RR and RT) increased in all groups of buffalo during the work period, but increases were greater in uncovered animals than in those covered with wet sacking. Similar differences occur in unshaded and shaded sheep (at temperatures of 45.8°C or 31.0°C respectively): ewes exposed to sunlight had a significantly higher RT (40.6 vs 40.1°C) and RR ($191/\text{min}$ vs $129.5/\text{min}$) than those in the shade (SIQUEIRA *et al.*, 1993).

2.8 The Effects of Exercise on Blood Constituents

Various blood tests during exercise and thermal exposure have been reported. For example, ACHARYA *et al.* (1979) found, in both crossbred (Holstein x Haryana) and Haryana bullocks, that there was an increase in haemoglobin %, PCV, total RBC and WBC counts after work; trends which could have resulted from loss of body water by such means as urination, defaecation and evaporation (sweating and respiratory) during work. Similar patterns were observed by KHALIL *et al.* (1990) in exercising sheep and MITTEN *et al.* (1995) in horses. On the other hand, GEORGIE *et al.* (1970) and WIENER *et al.* (1988) observed that both haemoglobin and PCV decreased after exercise in cattle and sheep respectively. Subsequently, WIENER *et al.* (1988) reported that PCV actually declined from 34.9 to 32.6% in sheep on a low plane diet, and from 38.3 to 37.0% in those fed on a high plane, during heat exposure. These decreases were in general agreement with the observations of SINGH *et al.* (1968) in Zebu cattle; SINGH *et al.* suggested that this phenomenon may have been due to the destruction of some

erythrocytes as a result of the stress of exercise. Subsequently, HAYS *et al.* (1978) found that both blood haemoglobin and PCV decreased (by 4.5% and 2.3% respectively) in calves exercised for 1h on a treadmill at a speed of 1.8 km/h and on a 10% slope. Similarly, in Sokoto Red goats, IGBOKWE *et al.* (1992) found that PCV decreased significantly from 32.1 ± 3.0 to $29.2 \pm 1.6\%$ when environmental temperature increased between 08.00 and 16.00h. This might have been due to sequestration of red blood cells in the capillaries following peripheral vasodilatation induced by environmental heat stress in the afternoon. Similar patterns were also reported by UPADHYAY and MADAN (1985), PEARSON and ARCHIBALD (1989).

In comparison, in humans the mean arterial blood pressure has been shown to increase by 19 and 57% during light and heavy exercise respectively (ERIKSEN and WAALER, 1994) as well as there being an increase in blood flow of from 2.0 to 3.2 litre/minute (SUNDBERG and KALLSER, 1992). Moreover, during exercise in cattle, GEORGIE *et al.* (1970) reported a significant decrease in blood glucose, but an increase in blood lactic acid. In addition, CHEN *et al.* (1993) pointed out that in rats both red blood cell and haemoglobin contents decreased after exercise, probably due to an increase in plasma volume (CONVERTINO *et al.*, 1980). BALSOM *et al.* (1994) also reported that haemoglobin concentration increased by about 15% after only 15 minutes of exercise at 20 km/h on a treadmill.

In general, PCV levels follow the law of splenic function (DOOLEY, 1973) whereby in sheep given an insulin injection the PCV increased by an average of about 40% in 110 min, PCV then declined to values that still exceeded the pre-injection values. A similar pattern is found in man, with an increase in PCV of 47% during 2 hours' exercise and a decrease of 45% after 10 minutes' rest (OHNO *et al.*, 1992). DETWEILER (1984) reported that with sympathetic neural activation during exercise, the spleen contracts and discharges erythrocytes into the circulation and increases the PCV. KUHLMANN *et al.* (1985) agree that the spleen is an important reservoir of erythrocytes, called upon when the body has a greater need for oxygen in the tissues, and that increases in PCV and hemoglobin concentration are critical mechanisms enabling

ruminants to increase oxygen transportation to exercising muscle. Those conclusions are supported by BIRD *et al.* (1981), MUNDIE *et al.* (1991) and APPLE *et al.* (1994).

BAUMGARTNER and PEINTHANER (1994) reported that there were significant seasonal differences in REC, PCV and haemoglobin concentration in sheep; for example, from winter to summer those parameters increased 2.1, 3.6, and 7.0% respectively. SINGH *et al.* (1980) reported that the values of blood base excess, plasma bicarbonate, standard bicarbonate and blood pH were all higher, and carbon dioxide tension was lower, as a result of exercise in buffalo. These changes indicate the possibility of animals suffering from alkalosis at both the respiratory and metabolic levels. PETHICK *et al.* (1991) reported the concentration of glucose in the arterial blood of sheep during exercise at different speeds on either a 0° or 90° incline to be as shown in Fig. 3.

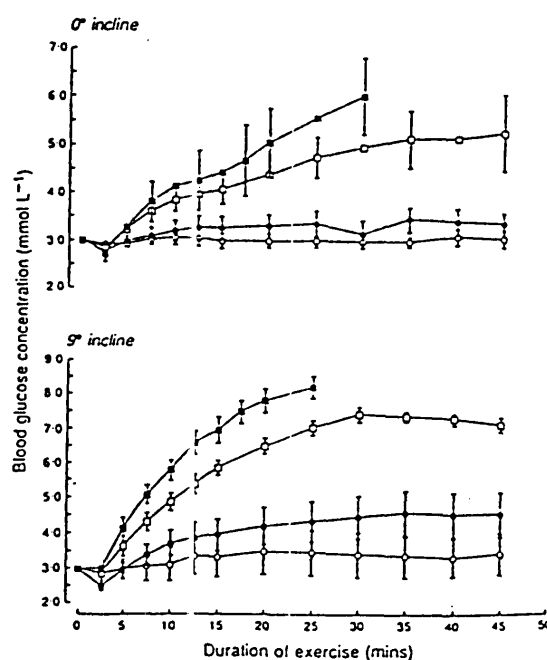


Fig. 3 Changes in the concentration of glucose in arterial blood during exercise at different speeds on either 0° or 90° incline (3 km/h ○—○, 5 km/h ●—●, 7 km/h □—□ and 9 km/h ■—■. Values are mean \pm s.e.m. for 5 sheep (After PETHICK *et al.*, 1991). Error bars in this and all subsequent figures represent the s.e.m. values for the respective groups.

These results suggest that the higher the speed, the higher the glucose concentration in arterial blood. For example, on a 9° incline and at treadmill speeds of 3, 5, 7 and 9 km/h, the concentrations of glucose in the arterial blood after 25 min of exercise were 34, 40, 68 and 83 mmol/l.

MILLER *et al.* (1963) found that the rates of fatty acid oxidation in dogs at rest and during exercise (6 km/h on a 15% slope for 25-30 minutes) were 11 ± 1.1 and 32.8 ± 1.4 $\mu\text{M/kg/min}$, while the rates of oxygen uptake were 8.6 ± 0.7 and 39.2 ± 3.3 ml/kg/min respectively. In addition, in man, HAVEL *et al.* (1964) reported that the FFA concentration increased from 0.62 to 0.93 $\mu\text{moles/ml}$ during exercise on a bicycle ergometer for 2 hours at a room temperature of 21-23°C.

From the above results it can be concluded that in accordance with the splenic function law, increases or decreases of both PCV and haemoglobin depend upon the duration of exercise. As a result, during short term exercise, the increase in PCV is due to more blood cells being released by the spleen. On the contrary, during long time exercise the flow of blood cells back to the spleen causes both PCV and haemoglobin to decrease; a progressive change which is taken to indicate acclimatisation.