FACTORS INFLUENCING THE ENERGY REQUIREMENTS OF NATIVE PONIES LIVING OUTDOORS IN THE UNITED KINGDOM.

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Declaration

The work reported in this thesis is my own, and the thesis is my own composition

signed__

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Abstract

The purpose of this study was to determine the daily energy requirements of ponies native to the U.K., living on upland areas. This information can be used to improve the management of ponies kept under these conditions.

The objectives of this thesis were to i) determine the effects of speed and terrain on the energy costs of ponies when walking, ii) measure seasonal differences in the hair coat, iii) estimate the effect of a wet winter coat on metabolic rate, iv) determine the proportion of a day spent by free-living ponies in feeding, walking, standing and lying, v) estimate the total distance moved daily by these ponies, and vi) describe the relationship between weather conditions and the behaviour and location of ponies.

In the first study, the energy costs of walking were measured in four Shetland and two Exmoor ponies by using open-circuit, indirect calorimetry. The energy cost of activity, above that for standing, was independent of speed and averaged 1.02 J/kg liveweight/m travelled. An Oxylog, a portable breath-by-breath oxygen analyser, was used to determine effects of terrrain on the energy cost of walking using five Shetland ponies. The mean (s.e.) energy expenditures (J/kg/m) were:- grass 1.7 (0.07); concrete 2.9 (0.15); 12 cm of mud 5.9 (0.21); uphill ($+5.8^o$) 5.5 (0.31); downhill (-5.8^o) 3.3 (0.23) J/kg/m.

In the second study, physical parameters of the winter and summer hair coats of six Shetland ponies were compared. Also, metabolic rate was monitored as a means of assessing the effect of wetting ponies in winter coat. Coat density in the winter averaged 96.2 (s.e. 8.01) mg/cm^2, 3.24 times the summer value of 29.5 (3.37) mg/cm^2. Fibre diameter differed significantly between ponies within season. For some ponies there were seasonal changes in fibre diameter. The number of fibres/cm^2 did not differ significantly between seasons. Metabolic rate (determined by open-circuit, indirect calorimetry) and body temperature were unaffected by wetting (to the skin) the dorsal surface of Shetland ponies in winter coat. However, there were decreases in skin temperature over the wetted area which suggested local vasoconstriction.

In the third study, six Exmoor pony mares, kept in an enclosed area of fell in Cumbria, were observed in late winter (W) when they were pregnant, and in summer (S) when they were lactating. There were significant seasonal differences in the time spent feeding 17.2 h (W), 13.5 h (S); walking 0.5 h (W), 1.2 h (S); and standing 4.6 h (W), 6.2 h (S); but not in lying 1.3 h (W & S). The total distance moved by the mares in 24 h; 3.1 - 5.7 km (W) and 3.7 - 4.9 km (S), was calculated as the sum of the distances moved whilst grazing and walking. In winter, ponies preferentially grazed facing directly into or away from the wind at all wind speeds, and preferred to stand in areas where wind speed was reduced. In the summer, the same orientations to the wind became evident at wind speeds of 5 m/s. Ponies stood in the most exposed areas during the hottest parts of the day, but stood in sheltered areas at night. Grazing speed and bite rate were significantly greater ($P<0.05$) in the winter than in the summer.

The results showed that the energy costs of activity (walking and grazing) were greater in winter than in summer. Therefore, seasonal adjustments in energy requirements are needed to allow for changes in activity as well as changes in heat loss. Recommendations are made regarding the management strategies for ponies kept outdoors.

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LIST OF ABBREVIATIONS

ANOVA	analysis of variance.
BE	bare earth.
BMR	basal metabolic rate.
bpm	heart rate beats per minute
C	centigrade.
cal	calories
CED	climatic energy demand.
cm	centimetres.
CO_2	carbon dioxide.
d	day.
DBT	dry bulb temperature.
DE	digestible energy.
d.f.	degrees of freedom.
E	energy.
Ew	energy cost of walking.
g	grammes.
GE	gross energy.
h	hours.
ha	hectares.
H.F.R.O.	Hill Farming Research Organisation.
HR	heart rate.
Hz	hertz.
J	joules.
J/s	joules per second = watts.
k	efficiency of utilization;
	k_m for maintenance, k_f for fattening, k_w for work.
kcal	kilocalories.
kg	kilogrammes.
kgm	kilogramme metres.
kJ	kilojoules.
km	kilometres.
kph	kilometres per hour.
l	litres.
LCT	lower critical temperature.
m	metres.

μm	micrometres.
MJ	megajoules.
mg	milligrammes.
min	minutes.
ml	millilitres.
mm	millimetres.
mmHg	millimetres of Mercury, (Atmospheric pressure).
n	number of observations.
NE	net energy.
O_2	oxygen.
P	probability.
p.e.	percentage error; standard error expressed as a percentage.
Q1 - Q3	interquartile range.
r	correlation coefficient.
r^2	coefficient of determination.
RH	relative humidity.
RHR	relative heart rate.
RMR	resting metabolic rate.
RQ	respiratory quotient.
s	seconds.
s.e.	standard error.
s.e.d.	standard error of difference.
SMR	standing metabolic rate.
SSR	shortest significant range.
STP	standard temperature and pressure.
STPD	standard temperature, pressure; dry.
TE	total energy cost.
TEw	total energy cost of walking.
TEwtg	total energy cost of walk, trot and gallop.
TNZ	thermoneutral zone.
UCT	upper critical temperature.
V	volume.
W	total body weight (kg).
W	watts.
WBT	wet bulb temperature.
WFR	water flow - rate.
WT	water temperature.

CHAPTER 1

INTRODUCTION

The breeding populations of native ponies kept on marginal land in the United Kingdom (U.K.) without supplementary feeding have been subject to concerns about their welfare due to sometimes fatal losses of body condition over the winter and spring. These ponies face some of the most rigorous of environmental conditions in the U.K., but studies have shown that they are well adapted to their habitats and can survive if not overstocked (Pollock, 1980; Gill, 1988; Lewis, 1991). Prediction of the daily energy requirements of ponies living outdoors could provide an important guide to assist in their management such as setting stocking densities for different types of range in different seasons.

The daily energy requirements of equids living outdoors are the sum of the energy costs associated with their maintenance and activity, which are affected by many different factors. In the case of free-living ponies, seasonal changes in climate and in the availability of food and water probably have the greatest influence on maintenance energy requirements. Other factors, such as parasite burden and disease, can be critically important as they influence the animal's ability to cope with the major seasonal variables. The reproductive performance of these ponies, the basis of their economic viability, depends on their ability to thrive in a constantly changing nutritional and thermal environment.

Herbivores in seasonal temperate zones inhabit areas where the patchy distribution of food is constantly changing in quality and quantity. The availability of water, total foraging time and the distances travelled each day are interdependent and therefore vary seasonally. Consequently, the daily energy costs of these activities also change. Locomotion is an important aspect of foraging, but the influence of natural ground surfaces, which are highly variable, on the energy costs of locomotion have not been investigated to any great extent in equids, unlike the influence of speed on the energy costs of horses.

Field biologists have reported on the association between ambient temperature, wind speed and the sheltering behaviour of feral horses. However, the benefit of shelter in terms of a measured reduction in wind speed, and therefore rate of heat loss, has not been recorded (Berger, 1986; Duncan, 1985). The changes in energy required for maintenance due to seasonal changes in ambient temperature and heat loss have been studied under controlled conditions by a few researchers (Ellis, 1975; McBride, Christopherson and Sauer, 1985; Cymbaluk, 1990).

The total daily energy requirements of ruminant livestock under various conditions of management; e.g. beef suckler cows and hill ewes; have been calculated as the sum of the energy costs of maintenance, production (growth, pregnancy, lactation) and the distance travelled daily (Agriculture and Food Research Council, 1993). Before this method can be applied to calculations of the daily energy requirements of ponies kept outdoors, information is needed on the energy costs of locomotion over various terrains and the distance travelled daily. The extent to which ponies are able to limit their energy losses to the environment by sheltering would also be an important consideration in such calculations.

The proportion of the equine population which lives outdoors all year round consists not only of the free-living ponies, but also of working animals. Those which are used for work are mostly kept on better farming land and receive additional feeding where this is necessary for them to maintain the required level of performance and body condition. At least 9500 ponies are kept under extensive management systems on traditional common grazings in breeding herds (Baker, 1994 and 1995). Although the administration of anthelmintics to these ponies is becoming more usual, the provision of supplementary fodder is rare and the only food and shelter available is that which the ponies can find within their normal range.

1.1 The development of Mountain and Moorland ponies in the U.K..

Fossil records have shown that the species *Equus caballus*, has existed in the British Isles since at least the last Ice Age (Ewart, 1900) and perhaps before. Bone fragments suggest that the height and weight of these animals were very close to those of the modern day Exmoor ponies, which are still kept in breeding groups on the area of moorland which gives them their name. Bennet (1992) described the Exmoor, and other British and Scandinavian breeds of pony, as modern descendants of the proto-draft sub-species *E. caballus caballus* (Linnaeus); animals physically adapted to cold winters, wet snow and a mixed terrain of firm and boggy ground.

Bennet (1992) suggested that the five sub-species of equid, recognised as the root-stock of the modern horse breeds, interbred where their ranges overlapped. In prehistoric Europe the annual migrations of equids must have increased this probability. Therefore, before the final closure of the British / European land bridge, ~ 7-8,000 years ago, there may have been some influence of Tarpan (*E. caballus gmelini*) and Warmblood (*E. caballus mosbachensis*) sub-species on the British proto-draft stock. The British Hill Pony, or Celtic Pony, then developed in isolation until immigrating humans brought continental stock with them (Bennet, 1992; Baker, 1993).

Ancient and recent historical changes in the socio-economic climate have provided both opportunities and pressures for the breeding of animals suited to particular roles (Bennet, 1992). Local mares, in the British case predominantly proto-draft stock, were crossed with sires which brought a mixture of influences from Oriental (*E. caballus pumpelli*), Tarpan (*E. caballus gmelini*) and Warmblood (*E. caballus mosbachensis*) sub-species. In their pure form, these sub-species were adapted to environments which were hot and dry (Oriental), glacial (Tarpan) and wet forest edge (Warmblood) (Bennet, 1992) and selection for specific traits resulting from these influences ultimately gave rise to the variation in phenotype and physiology seen in the modern breeds.

In 1896 the first concerted effort was made to describe and document the regional types of pony still in existence in the U.K. (Hendricks, 1995). Nine breeds were originally distinguished; Connemara, Dale, Dartmoor, Exmoor, Fell, Highland, New Forest, Shetland and Welsh, collectively described as native Mountain and Moorland (M&M) ponies. More recently the Eriskay and Lundy ponies have also been described (Hendricks, 1995). Of the M&M ponies, the Exmoor is agreed to have been least affected by influences from other sub-species (Baker, 1993), indeed Groves described it as a "...virtually pure-bred strain of aboriginal pony." (Groves, 1974). Hence there are direct connections between modern native ponies, particularly evident in the Exmoor pony, and animals which were adapted to cold and wet conditions long before the selective influences of domestication occurred.

1.2 Free-living ponies in the U.K.

Several breeds of pony are still bred in free-living groups on traditional ranges on marginal land in the U.K.. They inhabit localised areas of heath, moor, woodland, tidal marsh and hill from which they gain all their nourishment and shelter (Gill, 1994). Although the breeding and numbers of these animals are managed in terms of the selection of stallions and the removal of youngstock, these populations lead a relatively undisturbed existence with minimal intervention. However, because these animals are owned and managed, they are neither wild nor feral. To distinguish them from ponies kept in more controlled domestic situations they are usually described as free-ranging or free-living populations. As there are no feral equids in the U.K., free-living ponies have been of interest to researchers as they have enabled investigation of the sociology and ecology of ponies living under near natural conditions (Tyler, 1972; Clutton-Brock, Greenwood and Powell, 1976; Gates, 1979; Gordon, 1986; Albiston, 1987).

The population of free-living ponies in the U.K. was estimated to be 9,647 in 1994 (Baker, 1994), which was approximately 1.6 % of the total U.K. horse population according to 1992 figures (Cross, 1992). It is not known, and it is very difficult to estimate, how many of the remaining 98.4 % of horses remain outdoors for the entire year. The number of animals of each breed which were living under traditional extensive management, i.e. free-living, in 1994 are given in Table 1.1 (Baker, 1994 and 1995).

1.3 Management practices for free-living ponies

Free-living ponies are generally run on common grazings where the Rights of Common Pasturage, governing the numbers of each species of animal which can be run on the common, are attached to particular local agricultural holdings (Lewis, 1991). The administration of these commons varies between regions, but usually involves the payment of an annual fee per head of livestock to an elected organising committee which oversees the welfare of the animals and all matters pertaining to their management on the common. The common grazings used for ponies are predominantly in statutory conservation areas where government departments and specific conservation orders e.g. Sites of Special Scientific Interest, may have strong influence on land management policies and, as a consequence, on pony management.

Table 1.1; Estimated number of native ponies kept under extensive management in the British Isles and Ireland in 1994.

Breed	*Number*
New Forest	3800
Dartmoor (mixed ancestry)	2650
Connemara	1000
Welsh (Section A)	1000
Shetland	600
Fell	250
Exmoor	197
Dartmoor (registered)	100
Highland	50

Source, Baker (1994 and 1995)
Section A = height category of Welsh pony
registered = registered with the Dartmoor pony society

National Parks such as Exmoor, Dartmoor and the New Forest also attract large numbers of the general public and, while pressure generated by public concern over the condition of some ponies has been a beneficial force for change in terms of management practices (Pollock, 1980), road traffic accidents are the single greatest cause of death in free-living ponies (Gill, 1994). In an attempt to reduce these deaths several main roads through the New Forest have been fenced. Whilst this reduces the overall traffic accident problem it also effectively removes considerable acreages of grass from the forest thereby increasing grazing pressure on the remaining areas (Gill, 1994).

All free-living populations are gathered in at least once each year, mostly during the autumn when foals are old enough to be weaned and when the pregnant mares are less likely to be affected by capture and handling. The procedures followed after capture depend on the breed, but ponies are generally marked for identification, examined for registration purposes, dosed with anthelmintics and sorted for sale, re-release, or wintering off the common. Income is generated from the sale of animals, but little if any profit is realised (Gill, 1988). Partly for this reason, anthelmintics have only been regularly and widely used in the past decade since the provision of funds for this by charitable organisations such as the Royal Society for the Prevention of Cruelty to Animals (RSPCA) and the International League for the Protection of Horses (ILPH). Adult ponies in good condition usually attract the highest bids at annual local sales, but the majority of stock are sold as weanlings.

Common grazings tend to be in locations classified as Less Favoured Areas (LFA's) of agricultural land. Financial premiums available to support sheep and cattle production in these areas have never been available for pony production, which is not generally profitable. Some financial support is available to breeders of ponies on Dartmoor, via the Dartmoor Moorland Scheme or the Dartmoor Pony Support Scheme (Harrison, 1993) and to breeders of New Forest ponies via the Forest Fed premiums (Gill, 1991). Many individuals and both private and government organisations are involved in the practical and financial aspects of these schemes which have two main aims: 1, to improve the condition of animals living on the commons and 2, to encourage strong genetic links between the free-living populations and those bred away from their traditional proving grounds.

The management of free-living ponies has traditionally taken the seasonal variation in forage availability into consideration, by annually removing young stock not wanted for breeding and unfit animals in the autumn (Pollock, 1980). However, decreases in foraging area and large increases in pony numbers have significantly increased grazing pressure on most common grazings (Gill, 1994). As grazing pressure increases so does the probability that ponies will lose an unacceptable amount of body tissue over winter, or be unable to replace lost tissue in the following seasons due to decreases in carrying capacity during summer droughts or the delayed onset of herbage growth in cold, wet springs.

Overstocking, where this occurs, is not a simple problem to address in areas where the interests and influences of many groups have to be considered (Pollock, 1980). As far as individual animals are concerned, autumn / winter body condition scoring is likely to remain the most effective method by which the suitability of stock for re-release can be assessed. A general indication of the state of the population of ponies as a whole can also be gained from this procedure and, when used in conjunction with expert knowledge of the local habitat, can give an indication of the carrying capacity of the area (Pollock, 1980; Gill, 1991; Lewis, 1991).

Investigation of the energetics of locomotion and sheltering behaviour of native ponies, which are prerequisites for the application of current techniques of estimating the total daily energy requirements of domestic stock, should provide additional means of gauging the impact of the environment on the energy budget of these animals. Such information will also be relevant for ponies kept outdoors in a wide variety of situations, not just those living on moorland or forest.

1.4 Aim of this study

The aim of this study was to measure some unreported aspects of the locomotor and thermal energetics of free-living ponies relevant to the calculation of their daily energy requirements. The specific objectives of this thesis were to i) determine the effects of speed and terrain on the energy costs of ponies when walking, ii) measure seasonal differences in the hair coat, iii) estimate the effect of a wet winter coat on metabolic rate, iv) determine the proportion of a day spent by free-living ponies in feeding, walking, standing and lying, v) estimate the total distance moved daily by these ponies, and vi) describe the relationship between weather conditions and the behaviour and location of ponies.

In the concluding chapter the implications of the experimental findings are discussed as they apply to methods of predicting the energy requirements of ponies living outdoors.

CHAPTER 2

THE ENERGY COST OF LOCOMOTION FOR PONIES WALKING AT DIFFERENT SPEEDS AND OVER DIFFERENT TERRAIN

2.1 INTRODUCTION

The distance covered daily by free-living animals whilst foraging and travelling to water can be an important component of their total energy expenditure, especially when ground surface conditions are poor (Hudson and White, 1985). The aim of this study was to provide information which could be used for calculations of energy expenditure related to the movements of ponies kept under extensive management systems. This information could then be used to estimate the maintenance energy requirements of such animals (AFRC, 1993).

Maintenance energy requirements, as published by National Research Council (1989), include an allowance for "normal" activity in non-working animals, although the costs of such activity had not been measured *per se*. Published figures of the total daily energy requirements of horses have been calculated by adding the short term costs of work or exercise to these maintenance energy requirements (NRC, 1989). Whilst this may have been an appropriate method for estimating the total energy requirements of working horses, it is not appropriate for the free-living situation where the amount of food energy harvested is directly related to the time spent in physical activity, i.e. time spent in foraging.

The energy costs of foraging, other than costs associated with prehension, mastication, deglutition and digestion, can be attributed to the physical costs of locomotion (McDonald, Edwards, Greenhalgh and Morgan, 1995). The majority of data which have been published on the energy costs of locomotion in equids have been concerned with racing speeds and do not relate to grazing / foraging activity. Even when slower speeds have been included in these investigations, the use of natural ground surfaces rather than treadmills has been the exception rather than the rule (Kibler and Brody, 1945; Yousef and Dill, 1969a; Yousef, Dill and Freeland, 1972; Pagan and Hintz, 1986b). Of these few studies only Yousef *et al.*, (1972) calculated the influence of ground surface conditions (gradient) on the total energy expenditure of their donkeys.

The effects of different surface qualities on the energy requirements for locomotion on ground surfaces have not been investigated calorimetrically in equids. Because free-living ponies generally move slowly, and because they encounter different ground surfaces within their ranges (Pollock, 1980), the experiments in this chapter were designed to investigate, by using indirect calorimetry, the energy costs for ponies walking at different speeds and over different terrain.

2.2 LITERATURE REVIEW

2.2.1 Calorimetry and the study of bioenergetics

About 1800 years ago Galenos, a Greek physician to the Roman Emperor Marcus Aurelius, made important physiological deductions from his professional observations of gladiators. He predicted that the "vital substance" in air transferred to the blood in the lungs would one day be purified (Verworn, 1922, cited by Kleiber, 1961), but it took a further 16 centuries before this was achieved. In the 1780's, Lavoisier named Galenos's substance "oxygene" (acid forming) based on his observations of the production of heat and acid as a result of its use during combustion (cited by Kleiber, 1961). Lavoisier found that both digestion (of meat) and exercise produced heat (body heat) and acid (in urine) whilst utilising oxygen and concluded that metabolism was therefore also a combustive process (cited by Kleiber, 1961).

Heat, a by-product of both metabolism and combustion, has been recognised as a form of energy, and energy has been defined as the capacity of a system to do work (Lehninger, 1965). Therefore, a measure of the heat produced during work will give a measure of the energy used to do that work. Joule demonstrated that 426.3 kgm of work were equivalent to 1 kcal of heat which, in System of International Units (SI units), is equal to 4.184 kJ of heat (Poczopko, 1971). The term work can be used to describe physiological activity which can therefore be measured as the rate at which heat is lost from the body and be expressed as J/s (equivalent to watts).

The development of calorimeters, chambers in which animals can be totally confined to enable direct measurement of their rate of heat loss, has been described by McDonald *et al*. (1995). Comparisons of the rate of heat loss between animals in different physiological states have resulted in descriptions of e.g. basal metabolic rate and standing metabolic rate, heat increments of feeding etc. (Blaxter, 1989). This technique, termed direct calorimetry, is labour intensive and expensive to set up (McLean and Tobin, 1987) and has mainly been superseded by indirect calorimetric techniques.

Indirect calorimetry is based on measurement of the rates of consumption or production of respiratory chemicals; O_2, CO_2, methane, water and lactate. Direct relationships between the amounts of heat produced during combustion or metabolism and the volume of O_2 used and CO_2 produced were recognised very early in calorimetric research (Kleiber, 1961). The ratio of the volume of O_2 consumed to the volume of CO_2 produced, termed the respiratory quotient (RQ) can give an indication of the energy source; fat (0.71), protein (0.809) or carbohydrate (1.0) (Blaxter, 1989). Heat equivalents per litre of O_2 consumed and CO_2 produced can be used alone or in combination to calculate the total heat production of an animal (Brody, 1945; Brouwer, 1965). For example, when RQ = 1 the heat equivalents are 21.2 kJ/*l* for both O_2 and CO_2 (Blaxter, 1989). Tables are available which show the thermal equivalents of O_2

and CO_2 at different RQs (Brody, 1945). In order to facilitate comparison of data published as mlO_2 or calories with those in joules, the conversion factors 21.2 kJ/*l* O_2 and 4.184 J/cal have been used throughout this thesis.

Provided that respiration is predominantly aerobic, the relationship between energy expenditure and O_2 consumption will be linear over a range of submaximal workloads (Blaxter, 1989). This relationship has been described for ponies exercising at speeds up to 7m/s on a level treadmill (Hoyt and Taylor, 1981), and up to 9 m/s on an inclined (10 %) treadmill (Eaton, Evans and Rose, 1991). Therefore, aerobic respiration will predominate during slow-paced foraging activities.

Calorimetric techniques which compare the composition of exhaled gases to that of inhaled air may be either open or closed circuit. Open-circuit systems pull fresh air through a face mask, into which the animal breathes, at a constant rate calculated to collect all exhaled gases. The masks may be loose-fitting (Lawrence and Stibbards, 1990), or have one-way valves and be tight-fitting (Pagan and Hintz, 1986b). Such systems include gas flow meters and a means of sampling the air / breath mixture for either immediate or future analysis. Closed-circuit systems collect only exhaled gases, although they may simultaneously analyse fresh air, and require the use of tight-fitting face masks with one-way inflow and outflow valves (Brody, 1945; Blaxter, 1989).

Other indirect techniques, such as carbon and nitrogen balance, and dilution of radio isotopes of water, which do not involve collection of respiratory gases are discussed by Lawrence, Pearson and Dijkman (1991) and McDonald *et al.* (1995). These techniques are more appropriate for longer term studies of metabolic rate rather than the short term changes associated with studies of locomotion under controlled conditions.

2.2.2 Treadmills

Initial investigations into the energy requirements of equids were concerned with their requirements for maintenance, growth, locomotion and work (draught) (Brody, 1945). Motor-driven treadmills were used for these laboratory studies as they enabled investigators to exercise animals under controlled conditions beside the gas analysis equipment at a suitable range of speeds and with different draught loads. Although the use of treadmills has since given repeatability of experimental conditions for research into the energetics of locomotion, respiratory physiology and biomechanics (Snow, Persson and Rose, 1983), the artificial nature of the treadmill has always been acknowledged (Eaton, 1994).

Horses have been reported to acclimatise to treadmill exercise within one to two sessions (Fredricson, Drevemo, Dalin, Hjerten, Bjorne, Rynde and Franzen, 1983; King, Evans and Rose, 1995), and to show consistent stride parameters in trot and canter during repeated sessions (Ratzlaff, Grant, Rathgeber-Lawrence and Kunka, 1995). However, comparisons of the same animals trotting on ground surfaces and on treadmills have shown significantly increased duration of the stance phase in the forelimbs and greater caudal movement of both fore and hind limbs during retraction when on the treadmill (Buchner, Savelberg, Schamhardt, Merkens and Barneveld, 1994). Decreased stride length and increased stride frequency were measured in a horse unused to the treadmill (Fredricson *et al.*, 1983). A physiological comparison of horses ridden at a canter both on a track and on a treadmill reported that canter speed had to be increased by 10% on the treadmill, in comparison to the track speed, before plasma lactate levels and heart rate equated with track values (Sloet van Oldruitenborgh-Oosterbaan and Barneveld, 1995).

Sheep and cattle on treadmills have been demonstrated to gain physical support by leaning back on their tethers, resulting in significant reductions (55%) in their net energy costs of locomotion (Boyne, Brockway, Ingram and Williams, 1981). Whilst horses are not always tethered on treadmills it may be possible for them to gain some support from other attachments such as the gas collecting equipment.

As all of the published measurements of the energy costs of locomotion in ponies have been made using treadmills (Hall and Brody, 1934; Hoyt and Taylor, 1981; Al-Diwan and Lees, 1989; Eaton *et al.*, 1991), and taking the findings of the comparative studies mentioned above into consideration, it is possible that the available data for ponies would underestimate the energy cost of locomotion on ground surfaces. Field-studies of energy expenditure would be more appropriate for the collection of data applicable to both the free-living state and to working equids.

2.2.3 Measuring energy expenditure in the field

The simplest gas collection technique reported from field studies involved the collection of all exhaled gases, over a period of time, in bags virtually impermeable to respiratory gases such as meteorological balloons (Yousef, Dill and Freeland, 1972; Dailey and Hobbs, 1989). This technique has been used successfully to study the energetics of locomotion in donkeys (Yousef, Dill and Freeland, 1972) and various species of wild ungulate (White and Yousef, 1977; Dailey and Hobbs, 1989), but does require either immediate analysis on site or proficient methods of preserving aliquots of gases in the field to prevent their deterioration before laboratory analysis.

Pagan and Hintz (1986b) were able to take gas samples from horses exercising around an outdoor track by towing an open-flow system on a trailer around the track beside the horses. Gas collection was made through a face mask and aliquots of the gas samples were analysed later in the laboratory. The influence of the compacted, stone-dust track was taken as a normal factor in the overall cost of exercise and was not investigated separately (Pagan and Hintz, 1986b). To date, no such outdoor experiments have been reported for ponies.

Detailed field studies of the effects of different ground surfaces on the energy costs of walking in draught ruminants have been made by Dijkman (1993) and Fall (1995) and it was possible that the equipment used by these authors would be suitable for ponies. The Oxylog (Humphrey and Wolff, 1977; P.K. Morgan Ltd, Kent, U.K.), a portable, breath-by-breath, differential oxygen analyser designed for humans and adapted for large ruminants (Lawrence *et al.*, 1991), was used by these authors to make their measurements. The Oxylog used a flow meter to measure ventilation volume during inspiration whilst the expired gases were channelled through one O_2 analyser, and fresh air through the other. Lawrence *et al.* (1991) reported that the tight fitting face mask which this technique required was not easily accepted by animals, however, Dijkman (1993) had a high success rate in a later study when time was taken to introduce the mask gradually over several weeks.

Another problem may occur with this type of gas analysis equipment when animals pant to keep cool. During panting the ventilation volume may increase to the extent that the difference in O_2 concentration between inhaled and exhaled gas samples may be smaller than the resolution of the O_2 analysers. However, this problem was not reported to occur in cattle under climatic conditions normal to the U.K. (Dijkman, 1989), therefore the Oxylog would also be appropriate for field-use with ponies in the U.K..

2.2.4 Standing metabolic rate

The classic approach to measuring basal metabolic rate (BMR) has been to use a starved (postabsorptive), resting, i.e. lying, animal or human (Blaxter, 1989). Horses were trained to lie down for calorimetric investigations by Winchester (1943) and Brody (1945) who both measured the energy expenditure of lying and standing ponies. Neither found significant differences between the two positions (1.33-1.58 W/kg lying; 1.30-1.48 W/kg standing).

The data collected by Winchester (1943) showed a tendency for greater energy expenditure in the lying pony which the author attributed to respiratory compromise based on the significant increases in rates of respiration and ventilation which he observed. From Ruckebusch's (1972) observations that rapid eye movement (REM) sleep and complete muscle relaxation occur when horses are laterally recumbent, a decrease in metabolic rate may have been expected. Although Winchester's (1943) ponies had been trained to lie down from a young age and had previously been the subjects of a similar investigation (Brody, 1945), they were alert and tended to lie in the sternal position rather than laterally. These facts alone could explain Winchester's (1943) observations of increased respiration and ventilation rates although heart rate, which varies directly with energy expenditure (Eaton, 1994), was not observed to change. More subtle approaches to measuring metabolic rate in equids with free choice of lying or standing may yet demonstrate metabolic advantages of lying down.

In comparison to ponies, the energy requirement of cattle for standing was 10% greater than that for lying (Osuji, 1974). Brody (1945) proposed that lack of an incremental cost of standing in horses compared to cattle was a consequence of the greater relative strength in horses of the suspensory and check ligaments, part of the stay apparatus which mechanically supports the fore and hind limbs (Smythe, 1975). This proposal was not supported by reference or data and, although check ligaments are absent in cattle (Clayton and Flood, 1996), the comparative roles of other anatomical differences between the species in the support of body weight was not explored.

The fact that horses spend a very small proportion of their total resting time lying down (0.07) in comparison to cattle (0.67) (Arnold and Dudzinsky, 1978) may be related to their minimal incremental costs of standing. The positions of the joints in both the fore and hind limbs of standing equids are stabilised by their respective stay apparatus (Smythe, 1975), which consists predominantly of tendinous tissue working in apposition and which therefore have very low energy requirements (Smythe, 1975). All equids, whilst standing, have an ability unique amongst ungulates to lock one hind limb in extension whilst they rest the other. This is probably achieved by hooking the medial patellar ligament over the inner edge of the femoral trochlea (Smythe, 1975). Due to the reciprocal apparatus (Adams, 1987) this movement of the medial patellar ligament locks the knee (stifle) and the tarsal joint (hock) mechanically. Once this locking mechanism has been engaged the limb becomes a supporting prop requiring minimal energy expenditure, and the opposite limb can be flexed and rested on the toe of the hoof. An indication of the stability and ease of standing in equids was shown by the recording of slow wave sleep from horses which had adopted this resting position (Ruckebusch, 1972).

As BMR only gives the minimum energy costs needed to sustain life (Poczopko, 1971) it is not a measure which has practical application (Blaxter, 1989). Therefore, the standing metabolic rate (SMR) of normally fed animals is commonly used as a baseline rate in the calorimetric study of locomotion and work (Lawrence and Stibbards, 1990). The fact that there was no significant difference between lying and standing in the energy expenditure of experimental horses suggests that calorimetric measurements from standing horses would form a reasonable basis for comparison with measurements made during other activities.

The smallest adult ponies from which SMR has been measured weighed 125 and 206 kg (Pagan and Hintz, 1986a). As part of an investigation into the maintenance energy requirements of horses, these animals were confined in metabolism crates and fed a series of diets formulated at levels above and below their maintenance energy requirements (NRC, 1978). Metabolic rates were measured from each pony for each diet and SMR at zero energy balance (food energy in = energy requirements) was estimated as 1.15 and 1.16 W/kg (Pagan and Hintz, 1986a). Winchester (1943) and Brody (1945) have reported measurements of SMR for ponies which were higher at 1.30-1.48 W/kg, whilst the range of values reported by Hall and Brody (1934) for ponies weighing less than 350 kg, 1.06 - 1.52 W/kg, includes the values reported by the three previous papers.

Pagan and Hintz (1986a) proposed that, as their data were calculated for zero energy balance they therefore represented a minimal energy cost of standing. Whilst this may have been true for the two ponies they used, this may not be the case generally as their lowest value of 1.15 W/kg was 8.5% higher than Hall and Brody's (1934) lowest value of 1.06 W/kg.

Pagan and Hintz (1986a) calculated the SMR at zero energy balance for two horses (500 kg and 856 kg) as 0.93 - 0.94 W/kg in the experiment mentioned above. Other values of SMR in horses ≥ 500 kg include 1.08 - 1.34 W/kg (Hall and Brody, 1934); and 1.06 - 1.77 W/kg (Eaton, 1994). Because of the influences of excitement on such measures, Eaton considered 0.71 W/kg could be the BMR for a 500 kg horse. The SMR values described for horses and ponies were essentially the same.

A decrease in BMR with increasing body size has been demonstrated in mammalian species and led to metabolic body weight being adopted as a means of comparing BMR between species, even those differing in body weight by several orders of magnitude (Poczopko, 1971). The figure finally accepted was $W^{0.75}$ where W = total body weight (Poczopko, 1971). This relationship does not necessarily apply between individuals within a species (Blaxter, 1989) and Pagan and Hintz (1986a) suggested that, from their SMR data, $W^{0.87}$ may be the best relationship in horses. However, from their own work, and from that of Benedict (1938), Pagan and Hintz (1986a) concluded that $W^{1.0}$ was a sufficient basis for calculation of the energy requirements for maintenance of horses ranging in weight from 100 to 1,000 kg.

2.2.5 The net energy concept in energy costs

In the study of energetics it is possible to compare the energy costs of standing to those of different, incremental work loads measured in the same animal (Lawrence and Stibbards, 1990). Therefore the incremental (net) energy cost of walking (Ew) would be calculated by subtracting the cost of standing, in the same location, from the total (gross) cost of walking (Hall and Brody, 1934). This factorial approach allows daily variation in all uncontrollable variables; temperature, wind speed, temperament of the animal etc., to be taken into account by assuming that their effects on the metabolic rate of the animals whilst standing and exercising will be equal (Lawrence and Stibbards, 1990). Net energy costs may therefore be compared between experiments with greater confidence than measurements of the total energy costs of an activity.

Not all investigators have taken the net energy cost approach, some have only reported the total energy costs of each activity (Al-Diwan and Lees, 1989), while others only report the rate of O_2 use without converting to a unit of energy (Hoyt and Taylor, 1981; Eaton *et al.*, 1991). Comparisons between the findings of such experiments need to take all aspects of their experimental protocols into consideration regarding their possible influences on the results reported.

2.2.6 Energy expenditure during locomotion

Hoyt and Taylor (1981) studied the relationship between speed of locomotion up to 7 m/s and the total energy costs of locomotion on a treadmill in three small ponies (110-170 kg). By plotting the total energy cost/m travelled (ml O_2/m) at walk, trot and gallop, these authors demonstrated that for each gait there was a narrow range of speeds at which locomotion was least costly, and that these speeds were the ones normally used on ground surfaces by the one pony for which this comparison was made. The diminishing contribution of SMR/m was evident as speed increased and, once the normal, or comfortable (Lawrence and Stibbards, 1990), range of speeds in each gait were exceeded, the increasing costs associated with the use of an inefficient gait at that speed became apparent in an increase in energy cost/m. Whilst this curvilinear economy of locomotion illustrated the energetic basis for natural gait selection at certain speeds, Hoyt and Taylor (1981) found that, when data from the artificial speeds were excluded, a linear regression accurately described the relationship between speed (m/s) and the total costs of walk, trot and gallop (TEwtg; ml O_2/kg/min) in all three of their ponies.

Although Hoyt and Taylor (1981) were able to measure the speed of a pony exercising on the ground they were unable to make calorimetric measurements of energy expenditure under the same conditions. Therefore, the energy costs of locomotion on the ground were still unavailable for small equids. Pagan and Hintz (1986b) investigated these costs by exercising 4 horses (~500 kg) on a packed, stone-dust track and found that the relationship of TE over all speeds (up to 6.5 m/s) was best described by an exponential equation:-

$$\text{cal/kg/min} = e^{3.02 + 0.0065\ \text{m/min}} \qquad (r^2 = 0.92)$$

but could also be described by a linear equation:-

$$\text{cal/kg/min} = 5.57 + 0.449\ \text{m/min} \qquad (r^2 = 0.87)$$

On the basis that the exponential equation yields a realistic SMR for zero speed (1.43 W/kg) whilst the linear equation does not (0.39 W/kg), the exponential equation is appropriate for use in calculating the energy costs of walk at all speeds. However, the TE of walk (1.5 m/s) and trot (3.5 m/s) derived from this equation; 2.57 and 5.6 W/kg respectively, were lower than the costs measured by other authors in ponies exercising on treadmills (Table 2.1). There may be an effect of body size here, but when TE from thoroughbreds walking (4.46 W/kg) and trotting (9.66 W/kg) on a treadmill (Eaton, 1994) were compared with Pagan and Hintz's (1986b) horse data they were still lower than expected.

Table 2.1; The total energy cost of locomotion (J/kg/m) in ponies less than 400 kg liveweight exercising on level treadmills, as reported by several authors.

Treadmill Speed (m/s)	*Total energy cost (W/kg)*	*Total energy cost (J/kg/m)*	*Liveweight (kg)*	*No. of ponies*
0.5	1.90 [1]	3.80	280 - 290	1
0.5	1.82 [3]	3.63	140	1
0.97	2.41 [1]	2.48	280 - 290	1
0.98	3.04 [2]	3.10	~350	4
1.0	2.29 [3]	2.29	110 - 170	3
1.38	3.59 [2]	2.60	~350	4
1.39	3.50 [1]	2.52	280 - 290	1
1.8	5.44 [2]	3.02	~350	4
3.0	7.08 [4]	2.36	~340	9
3.0	7.53 [3]	2.51	110 - 170	3
5.5	14.03 [3]	2.55	110 - 170	3
10	27.2 [4]	2.72	~340	9

[1] Hall and Brody (1934);* from kcal/day. [2] Al-Diwan and Lees (1989);* from kcal/100kg/km.

[3] Hoyt and Taylor (1981);** from mlO_2/s and mlO_2/m. [4] Eaton et al. (1991);** from ml O_2/kg/min.

* 1 cal = 4.184 J ** 1 mlO_2 = 21.2 J (assuming RQ = 1).

This expectation was based, not only on the available data for horses of a similar size (Eaton, 1991), but also on the physiological differences measured between horses working on treadmills and on ground surfaces at the same speed, discussed in section 2.2.2. The assumption being that information available for horses suggests that the energy costs of walking on the ground would be higher than for walking on a treadmill.

Research on draught oxen indicates that the reverse may be true. Fall, Pearson and Lawrence (1997) reported that field measurements of the Ew/m on firm tracks were lower at 1.0 J/kg/m than the costs for walking on treadmills as measured by Brody (1945) at 1.9 J/kg/m and Lawrence and Stibbards (1990) at 2.1 J/kg/m. Fall et al. (1997) suggested that the oxen working on the treadmill may have been more anxious due to their unnatural situation and therefore have had higher costs than animals walking on a normal ground surface.

Therefore, it may be that the data from treadmill experiments is artificial and that the linear relationships between TE and speed of locomotion derived from the data are also artificial, even though they are widely accepted (Hoyt and Taylor, 1981; Blaxter, 1989). However, further comparisons of the exponential equation (Pagan and Hintz, 1986b) at galloping speeds (6.5 m/s) 18.01 W/kg, with the costs for ponies (Table 2.1) and thoroughbreds (16.9 W/kg, Eaton et al., 1991) show closer agreement than for walk and trot. If the exponential equation is used to predict the TE of horses galloping faster than 6.5 m/s the predictions no longer show agreement, e.g. at 8 m/s the predicted TE is 32.4 W/kg compared to measurements of 16.96 (Eaton et al., 1991) and 18.4 W/kg (Eaton, 1994). The differences may therefore be due to the mathematical differences between exponential and straight lines when used to describe the same data set.

If a straight line and an exponential line are used to describe the same set of data, the exponential line will lie above the straight line at the lower and upper extremes, but will lie below the straight line at some intermediate point. This is demonstrated when the linear and exponential equations describing Pagan and Hintz's (1986b) data are compared at SMR, walk (1.5 m/s), trot (3.5 m/s) and gallop (6.5 m/s); linear vs exponential; SMR, 0.39 vs 1.43 W/kg; walk, 3.21 vs 2.57 W/kg; trot, 6.96 vs 5.6 W/kg; and gallop, 12.6 vs 18.03 W/kg.

As the exponential equation published by Pagan and Hintz (1986b) for speeds up to 5.83 m/s appears to fit their data set more accurately than the linear equation, it could be accepted for calculation of values at walk and trot on that type of surface. However, further measurements should be taken from horses working on the ground over the entire range of galloping speeds commonly used by horses, i.e. up to racing speeds, to derive a more accurate equation for this gait. The same is true for all gaits on different surfaces and different sizes of horse.

The adult body weight in *E. caballus* ranges, approximately, from 100 kg to over 1000 kg and selection for different athletic traits has resulted in different physical types. Gunn (1983) made an anatomical comparison between horses selected for speed (thoroughbreds) and other breeds (including draught and Shetland) and found that the main anatomical difference was that the proportion of total hindlimb weight around the hip was greater in horses selectively bred for speed. This was considered to facilitate a higher stride frequency and to decrease the effort (energy) required to move the limb and thus result in a faster running speed (Gunn, 1983). It might be expected from this that differences would be seen between breeds in their rate of energy expenditure during locomotion. However, Eaton *et al.*, (1991) found no significant differences between the total energy expenditure of ponies of undeclared breeding (~340 kg) and of thoroughbred horses (~500 kg) exercising on both level (3 - 12 m/s) and sloping treadmills (+10%; 2 - 9 m/s). The only other study to include animals of significantly different body weights was that of Hall and Brody (1934) in which the energy expenditure of a Percheron gelding (687 kg) and a Shetland gelding (270 kg) when walking were compared. It was found that body weight did not have a significant effect on either TEw or Ew/m, although the authors were cautious about making a firm conclusion because of the small number of animals (Hall and Brody, 1934). When the data from a second Shetland pony used in the study were included in this comparison, the difference between the two Shetlands was greater than the difference between breeds. However, Hall and Brody (1934) did mention that the second Shetland had a sore shoulder and that this probably increased the energy cost of walking in this animal and could explain the difference between the two Shetlands.

When the net energy cost is calculated per m travelled (J/kg/m) it is independent of speed within the normal range of speeds in each gait, (Hall and Brody, 1934; Lawrence and Stibbards, 1990). Because use of the normal ranges of speed can be assumed for free-living animals (Pennycuick, 1975), and because it is difficult to measure their actual speed, Ew/m (J/kg/m) is an appropriate unit for calculation of the energy costs of locomotion when the distance travelled can be estimated. The only study to calculate Ew/m in horses by measurement of SMR and the total energy cost of walking (TEw) at a range of speeds was that of Hall and Brody (1934) where the two Shetland ponies and one Percheron were the only animals used over all speeds. Therefore, further studies were needed to clarify the net energy costs of walking for horses of different sizes. Al-Diwan and Lees (1989) measured the TEw for Welsh ponies (~350 kg) then calculated the net energy cost of walking by subtracting maintenance energy costs published by NRC (1978) from their measured values. As the NRC (1978) values included an allowance for normal maintenance activity, estimated as 29.1% of SMR by Pagan and Hintz (1986a), the incremental (net) energy costs of activity derived in this way by Al-Diwan and Lees (1989) would tend to underestimate energy requirements. The energy allowances for exercise published by NRC (1989) were based on the costs of exercise in horses reported by Pagan and Hintz (1986b), and which have been compared earlier in this chapter to costs in ponies and found to be significantly lower. Therefore the energy costs of locomotion in small ponies still needed to be clarified to enable accurate estimates of the costs of work, particularly on ground surfaces.

2.2.7 The energy costs of moving up and down gradients

Blaxter (1989) reported that the cost of moving 1 kg up 1 vertical m was fairly constant in mammals at 27 J/kg/m. Yousef, Dill and Freeland (1972) measured the energy costs in donkeys of climbing and descending gravel roads of different gradients, and found costs ranging from 17.2 to 29.3 J/kg/vertical m (Table 2.2). From extensive studies of donkeys it was concluded that the energy costs of locomotion on level surfaces for donkeys were not significantly different from those for horses (Mueller, 1996). Therefore, the variation from the standard 27 J/kg/vertical m seen in the donkeys may also occur in horses walking on different gradients.

Eaton et al. (1991) and Eaton (1994) presented, in graphic form, the total energy costs from walk to gallop (TEwtg) in ponies and horses working on treadmills at gradients of zero, +5% and +10%. By subtracting the costs for level locomotion from the costs on the gradients, the net energy costs to these animals for walk (1.5 m/s), trot (3.5 m/s) and gallop (8 m/s) were calculated per vertical m and per m travelled (Table 2.2). The net energy costs of trotting (2-6 m/s) up three gradients were investigated in small ponies (~140 kg) by Gonzalez (1990) and found to be higher than those for horses and larger ponies (Table 2.2). Although the values for horses and ponies were different from those of donkeys, they also varied from the standard 27 J/kg/vertical m given by Blaxter (1989).

When moving down hill animals utilize their potential energy due to gravity as a motive power and thereby reduce their energy costs of locomotion (Blaxter, 1989). This occurs up to a certain negative gradient, as yet undefined, beyond which the costs of preventing falling outweigh the energetic benefits of working with, rather than against, gravity (Eaton, 1994). The decreasing advantage of walking down increasingly steep gradients can be seen in the Ew/vertical m of donkeys walking down gradients of -2% to -17% where the cost-benefits decreased from -16.13 to -1.97 J/kg/vertical m. The same energy costs expressed as Ew/m travelled were 1.29, 0.65 and 1.29 J/kg/m (Yousef et al., 1972), which, in combination with the measurements made by Dijkman (1992), indicate that gradients between -10% and -15% are the most economic for donkeys.

2.2.8 The effects of ground conditions on the energy cost of locomotion

The additional costs of locomotion due to ground conditions have been measured in both domestic and wild ungulates. Different dry soil types increased the walking costs of oxen to 1.47 - 1.76 J/kg/m (Dijkman, 1993; Fall, 1995) compared to the costs of walking on firm tracks which were 1.0 - 1.34 J/kg/m (Becker, Rometsch, Susenbeth, Roser and Lawrence, 1993; Fall, 1995). On soft ground, i.e. after ploughing (Fall, 1995), on wet, boggy ground (Dijkman, 1993; White and Yousef, 1977) and in deep snow (Dailey and Hobbs, 1989) Ew has been measured to increase by variable amounts up to 500%. The deeper the animal sinks in relation to its leg length, in this case brisket height not shoulder height, the greater the costs incurred. The energy costs of equids for travelling on natural ground surfaces have not been investigated but, from the data shown here for other ungulate species, costs may be considerable.

Table 2.2; The net energy costs for equids (J/kg/m; per vertical m and per m travelled) of climbing and descending different gradients at walk, trot and gallop.

Uphill	*Gradient*	*+2%*	*+3%*	*+5%*	*+6.7 %*	*+10%*	*+13 %*		*+17%*
J/kg/vertical m	**walk (1.43 m/s)**	**17.2^1**				**21.2^1**			**29.3^1**
	(1.5 m/s)			**24.8^2**		**35.0^2**			
	trot (2-6 m/s)		**23.42^5**		**44.75^5**		**54.82^5**		
	(3.5 m/s)			**19.10^2**		**25.20^2** **27.10^3**			
	gallop (8 m/s)			**29.0^2**		**28.83^2** **21.49^3**			
J/kg/m travelled	**walk (1.43 m/s)**	**2.37^1**				**3.88^1**			**7.77^1**
	(1.5 m/s)			**3.27^2**		**5.49^2**			
	trot (2-6 m/s)		**3.43^5**		**5.09^5**		**9.09^5**		
	(3.5 m/s)			**3.31^2**		**4.85^2**			
	gallop (8 m/s)			**3.58^2**		**4.98^2**			
Downhill	***Gradient***	**-2%**				**-10%**		**-15%**	**-17%**
J/kg/vertical m	**walk**	**-16.13^1**				**-9.79^1**			**-1.97^1**
J/kg/m travelled	**walk**	**1.29^1**				**0.65^1** **0.55^4**		**0.67^4**	**1.29^1**

[1] Yousef et al. (1972) Donkeys; [2] Eaton (1994) Thoroughbreds; [3] Eaton et al. (1991) Thoroughbreds and ponies (~340 kg); [4] Dijkman (1992) Donkeys.

[5] Gonzalez (1990) small ponies (~140 kg).

2.2.9 Heart rate as an indicator of energy expenditure

Because of the difficulties associated with measuring oxygen consumption in the field, heart rate has been used as a convenient guide to the relative energy costs of moving over different ground surfaces (Erickson, Erickson, Sexton and Coffman, 1987; Sloet van Oldruitenborgh-Oosterbaan *et al.*, 1993). Simultaneous measurements of energy expenditure and heart rate in draught ruminants (Richards and Lawrence, 1984; Sneddon, 1986) and horses (reviewed by Eaton, 1994) have suggested that the increase in heart rate associated with doing work could be used to give accurate estimates of energy expenditure in previously calibrated animals. Heart rate monitoring equipment designed for horses has become relatively inexpensive yet robust (Sloet van Oldruitenborgh-Oosterbaan, van den Hoven and Breukink, 1988) and may offer a means of extending field studies of energy expenditure in situations where the heart rate of experimental animals can be calibrated against their metabolic rates.

2.2.10 Outline of this study

In order to increase the information available on the incremental cost of exercise in small ponies the energy costs of standing and walking were measured in Shetland ponies for a range of speeds up to and including the normal walking speed of these animals. In order to control walking speed accurately the animals walked on a treadmill at predetermined speeds (Experiment 1). Similar measurements were made with Exmoor ponies which walked around a circular race outdoors. Gas samples were collected and analysed, in the first experiment, using an open-flow indirect calorimetric system (Lawrence and Stibbards, 1990).

A portable, breath-by-breath, differential oxygen analysis system, Oxylog (Dijkman, 1993; Fall, 1995), was used in the second experiment of this study to investigate the effects of terrain on the energy cost of walking in Shetland ponies. The energy cost of locomotion on a treadmill (Experiment 1) was compared to that of locomotion on different ground surfaces (Experiment 2). Heart rate was monitored during Experiment 2 and investigated as an indicator of the energy costs of locomotion.

2.3 EXPERIMENT 2.1. THE ENERGY COSTS FOR SHETLAND AND EXMOOR PONIES OF STANDING AND OF WALKING AT DIFFERENT SPEEDS

2.3.1 INTRODUCTION

The information available on the energy costs of standing and of walking in ponies is limited. This information could form the basis for estimations of the energy expenditure of free-living ponies which, in the U.K., vary in size from the Shetland pony (~200 kg) to the Highland pony (~500 kg). Information is already available for horses of a similar body weight to the larger ponies, therefore the following experiment was designed in which the total energy costs of standing and of walking were measured in Shetland and Exmoor ponies (~300 kg).

The Shetland ponies walked on a treadmill where their walking speed could be maintained at a steady pace at speeds up to their normal walking speed. Such slow speeds are used when animals move whilst grazing and are therefore appropriate for estimations of the energy expenditure of free-living ponies. The Exmoor ponies walked around a circular, concrete race at their normal walking speed.

2.3.2 MATERIALS AND METHODS

2.3.2.1 ANIMALS AND THEIR MANAGEMENT

The ponies used in this experiment are described in Table 2.3. They were loose-housed in two breed groups in straw-bedded pens in an open-sided barn. The animals were fed good quality meadow hay to maintenance energy requirements (NRC, 1989) in two equal portions at 08:00 h and 16:00 h. Water and mineral licks were available at all times and a regular programme of de-worming and foot-trimming was followed. The Shetland ponies were given thirty minutes exercise, at liberty, five days per week in an indoor arena. The Exmoor ponies were exercised daily for half an hour using a horse-walker set at their normal walking speed of 1 m/s.

Table 2.3; **Details of the ponies used in Experiment 2.1.**

Animal	*Breed*	*Age (years)*	*Sex*	*Height (cm)*	*Weight (kg)*
1	**Shetland**	**2**	**Stallion**	**92.5**	**110**
2		**2**	"	**87.5**	**110**
3		**2**	"	**92.5**	**126**
4		**8**	**Gelding**	**102.5**	**232**
5	**Exmoor***	**14**	"	**125**	**334**
6		**18**	"	**130**	**322**

* No age effect on SMR or TEw has been reported for older horses (McKeever and Malinowski, 1997).

2.3.2.2 TRAINING OF THE ANIMALS

All the ponies were trained, over a period of two weeks, to wear the loose-fitting face mask (2.3.3.3) used for gas collection.

During this period the Shetland ponies were trained to stand quietly or walk (0.6 - 1.12 m/s) on the treadmill. Throughout the training period, and the following experiments, Shetland ponies were used in companion pairs; Nos. 1 and 2, and Nos. 3 and 4.

Two Exmoor ponies were trained to stand quietly and to be led at a walk around the circular race. The tubing which connected the face-mask to the pump was attached to the draught bar, therefore the animals had to accept the draught bar being pushed close behind them.

2.3.3 EQUIPMENT AND MEASUREMENTS

2.3.3.1 THE TREADMILL

A flat-bed treadmill with a variable speed control and a maximum speed of 2.5 m/s was used. Distance was estimated by automatically counting belt revolutions using a distance counter comprised of a mechanical tally counter which was triggered once per revolution by a wedge glued to the edge of the belt.

2.3.3.2 THE CIRCULAR RACE

The circular race, a circular concrete path 2 m wide within two low concentric brick walls with radii 3 and 5 m respectively (circuit distance ~25.5 m), was located in a field close to the laboratory (Figure 2.1; Plate 2.1a). It had been designed for calorimetric experiments with draught animals therefore a radial draught bar extended from a central pivot across the path. This had to be pushed behind animals not in draught.

2.3.3.3 MEASUREMENT OF RESPIRATORY GASES

An open-flow system was used for collection and analysis of respiratory gases (Figure 2.1). Ponies wore a loose-fitting face mask constructed from a 5 *l* (Shetlands) or 8 *l* (Exmoors) plastic bucket which was padded at the top with strips of foam rubber and secured to the pony with two 5 cm wide nylon straps. These straps passed from both sides of the bucket and fastened together with velcro behind the ears of the animal.

Air and exhaled breath were drawn together from the front of the mask by a multistage centrifugal pump powered by an induction motor (ASEA MT motor-IEC34 PSC). Two flow meters were used to measure the resulting airflow rates. A mass flow meter ('Hastings', Teledyne Raydist, Virginia, USA) was used as part of the treadmill system, whereas a Rotameter was used on the circular race (Dijkman, 1989). Both instruments were calibrated using a CO_2 dilution technique (Dijkman, 1989). Airflow was set at a rate which maintained excurrent CO_2 concentrations below 1% thereby ensuring that respiration rate would not be affected if re-breathing should occur (350 *l*/min).

Peristaltic pumps (Honeybourne Pumps Ltd, 113.015.503.0) drew two gas samples for analysis, one from the main airflow (animal) and one directly from the treadmill room or circular race (reference). These samples were dried in separate sets of apparatus by passing them through concentrated sulphuric acid, then a drying column containing magnesium perchlorate and calcium chloride with a silica gel moisture indicator.

Both reference and animal gas samples were analysed in parallel in a paramagnetic, differential O_2 analyser (OA184, Taylor Servomex Ltd. Sussex, U.K.) the scale of which was calibrated to zero with a standard O_2-free-nitrogen (British Oxygen Company, BOC) and to maximum with atmospheric O_2 (20.9%). The difference in O_2 concentration between the 2 samples was converted to an output signal by the O_2 analyser.

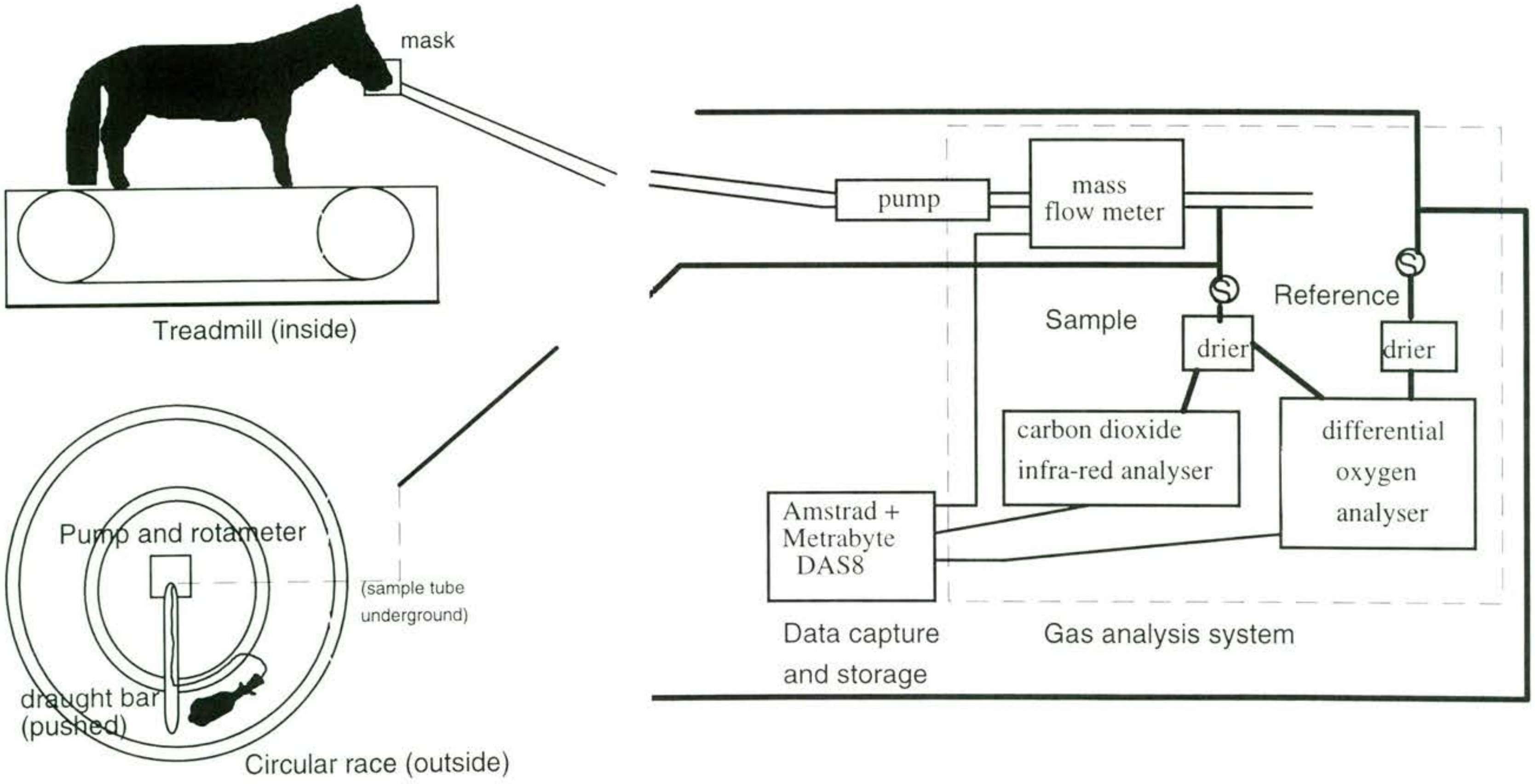
For measurement of CO_2 concentration, part of the gas sample from the animal was channelled through an infra-red CO_2 analyser (Ingra 2001, Grubb Parsons Ltd. Newcastle, U.K.) which was calibrated using O_2-free-nitrogen and a standard gas of known CO_2 concentration (0.943%, BOC) (Richards and Lawrence, 1984).

Output signals from the O_2 and CO_2 gas analysers were amplified and sampled at 5 Hz by a modified Amstrad personal computer (PC). Values were averaged for each consecutive period of 20 seconds, using the same PC, and stored on disc. The O_2 and CO_2 levels were displayed in real-time on the PC's monitor and regularly checked during each experiment.

The wet and dry bulb temperatures of the airflow were measured near the point where the samples were drawn off for analysis. Atmospheric pressure was recorded from a mercury barometer. These measurements were used during final calculations to correct gas volumes to standard temperature and pressure (0 °C, 760 mmHg).

A detailed description of this open-flow system, including calibration of the equipment, is given by Dijkman (1989).

Figure 2.1; **Schematic diagram of the open-circuit gas analysis system, treadmill and circular race.**



2.3.3.4 MEASUREMENT OF WALKING DISTANCE AND SPEED

Treadmill:-

The total length of the treadmill belt was multiplied by the number of revolutions of the belt completed during each walking session to give the distance travelled by a pony. Timing of each walking session was synchronised with the beginning of belt revolutions. This enabled accurate calculation of the speed during each walking session.

Circular race:-

The distance the ponies walked around the circular race was calculated by multiplying the figure given by an odometer, which was pulled around the top surface of the inner wall (Plate 2.1b), by a factor which corrected for the difference between the circumferences travelled by the pony and the wheel of the odometer. The walking period was timed (s) and the total distance (m) divided by time to give walking speed (m/s).

2.3.3.5 MEASUREMENT OF STRIDE LENGTH AND FREQUENCY

Strides were counted, as the number of times that a particular foot touched the ground, over a timed period. At least 100 strides were counted. It was then possible to calculate stride length and frequency from the known walking speed.

2.3.3.6 MEASUREMENT OF NORMAL WALKING SPEEDS IN SHETLAND AND EXMOOR PONIES

The null hypothesis, that the normal walking speeds of the Shetland and Exmoor ponies (Table 2.3) were not different, was tested by experiment (Appendices 2.1 and 2.2). As no significant differences were found ($P>0.05$) this hypothesis was not rejected. The mean (s.e.) walking speed of the Shetland ponies was 1.11 (0.012) m/s, and that of the Exmoor ponies was 1.18 (0.023) m/s.

Plate 2.1a; An Exmoor pony being led round the circular race whilst the draught bar is pushed behind it. The pony is wearing a flow-through face mask for collection of respiratory gases. The central air pump is visible on the right.

Plate 2.1b; The odometer, the small wheel on top of the inner wall, used to measure the distance a pony walked.

2.3.4 PROTOCOL

The same protocol was followed using the treadmill and the circular race. Measurements of respiratory gases were made whilst the animal:-

- stood for at least 20 min,
- walked at a constant speed* for at least 20 min,
- stood for at least 20 min,
- walked at a constant speed* for at least 20 min.

* = the same speed

Gas analysis and recordings were made for 20 min before and after the animals were exercised and continued for 20 minutes after the ponies were removed to allow calculation of drift in baseline O_2 and CO_2 concentrations.

A record of the behaviour of the pony was kept, with reference to the elapsed time of the experiment, to enable periods of additional activity, e.g. defecation or restlessness, to be correlated with deviations from steady state levels of VO_2 and VCO_2.

2.3.5 EXPERIMENTAL DESIGN

Shetland ponies:-

Individual ponies completed one replicate of the protocol (one session) per day. However, they could also act as a companion, tethered in sight of the exercising pony, during a second session. Ponies always worked with the same companion and were used in the order No.1,3,2,4.

Period 1:- Walking speed was allocated at random until each pony had completed 3 sessions walking at 0.63, 0.87, and 1.12 m/s.

Period 2:- Each pony completed, in sequence, 6 sessions at 0.35 m/s, 3 sessions at 0.63 m/s, 3 sessions at 0.87 m/s and 3 sessions at 1.12 m/s.

The total number of sessions completed on any day varied between 1 and 3 therefore each pony completed sessions at all times of day, effectively incorporating any effects of time of day into the experimental design.

Exmoor ponies:-

Both ponies completed six sessions of walking at the same speed, one per day, on the circular race. They worked without a companion.

2.3.6 CALCULATIONS OF ENERGY EXPENDITURE

2.3.6.1 CALCULATIONS OF TOTAL ENERGY EXPENDITURE

Values of O_2 and CO_2 concentration were graphed against time. Any deviations from steady state VO_2 and VCO_2 were compared against the behaviour record and not included in the computation of mean VO_2 and VCO_2 used in the calculation of energy expenditure.

The total energy costs of standing (SMR) and walking (TEw) were calculated as rates of energy expenditure derived from the steady state rates of O_2 consumption and CO_2 production (*l*/min., STPD). The following equation (Brouwer, 1965) was used:-

$$\text{energy expenditure (watts)} = (VO_2 \times 270.5) + (VCO_2 \times 82.7)$$

SMR and TEw were then expressed in terms of kg bodyweight as W/kg.

2.3.6.2 CALCULATION OF THE ADDITIONAL ENERGY EXPENDITURE FOR WALKING

For this calculation the assumption was made that the additional energy required by the animal for locomotion was additional to its energy requirements whilst standing. Therefore, this additional requirement described as the net energy for walking Ew (J/kg/m) = (TEw - SMR)/(liveweight x speed) where TEw and SMR are in watts, liveweight is in kg and speed is in m/s.

In the calculation of Ew it was assumed that day-to-day variations in the environment and in the animal would affect TEw and SMR equally.

2.3.7 DATA HANDLING AND STATISTICAL ANALYSIS

The linear regression equations describing the relationships between stride parameters and speed for Periods 1 and 2 were compared by calculating the 95% confidence intervals (95% CI) for the standard error of their differences (s.e.d.; Bland, 1995). SMR, TEw and Ew (Appendix 2.3) were subjected to a General Linear Model analysis of variance (GLM ANOVA; Minitab 9.2, 1994; Fall, 1995). Significant differences were explored within factor, e.g. animal or speed, by using the Shortest Significant Range (SSR; Parker, 1979).

2.3.8 RESULTS FOR SHETLAND PONIES

2.3.8.1 Stride parameters

Speed 1, the lowest speed, was not used in Period 1 therefore stride parameter data for speeds 2, 3 and 4 were used as the basis for comparisons between Periods 1 and 2 (Figures 2.2a and b; Appendix 2.3).

Stride length

Stride length decreased with increasing speed in Period 1 but increased with increasing speed in Period 2. The least-square linear regression equations (below), describing these relationships had high coefficients of determination as well as opposite signs for the gradients, therefore their obvious differences were not compared statistically.

Period 1 stride length (m) = 1.25 - 0.453 m/s $r^2 = 0.76$

Period 2 stride length (m) = 0.702 + 0.115 m/s $r^2 = 0.73$

Stride frequency

Stride frequency increased with increasing speed in both periods but showed different relationships which were described by the equations:-

Period 1 stride frequency (strides/min) = 11.4 + 26.7 m/s $r^2 = 0.98$

Period 2 stride frequency (strides/min) = 37.4 + 8.86 m/s $r^2 = 0.78$

The difference between Periods 1 and 2 was significant ($P<0.05$); the s.e.d. = 17.84 with a 95%CI = 17.48 to 18.20 (Bland, 1995).

When speed 1 was included in the regression analysis of Period 2 (Figure 2.2b), the resulting equations were:-

stride length (m) = 0.503 + 0.49 m/s $r^2 = 0.88$
stride frequency (strides/min) = 19.0 + 40.9 m/s $r^2 = 0.92$

Figure 2.2a; The relationship between treadmill speed (m/s), stride length (m) and frequency (strides/min) measured with four Shetland ponies during Period 1 of Experiment 2.1.

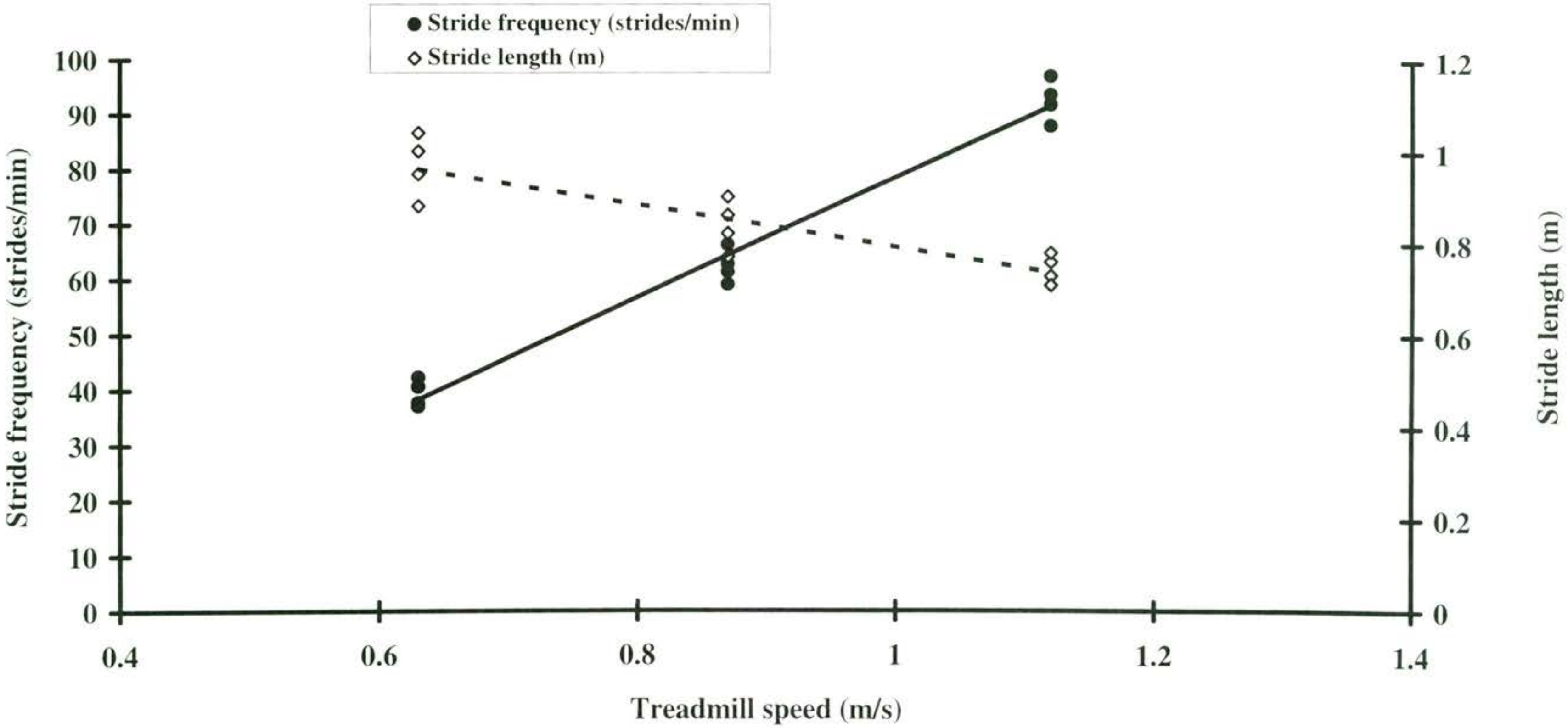
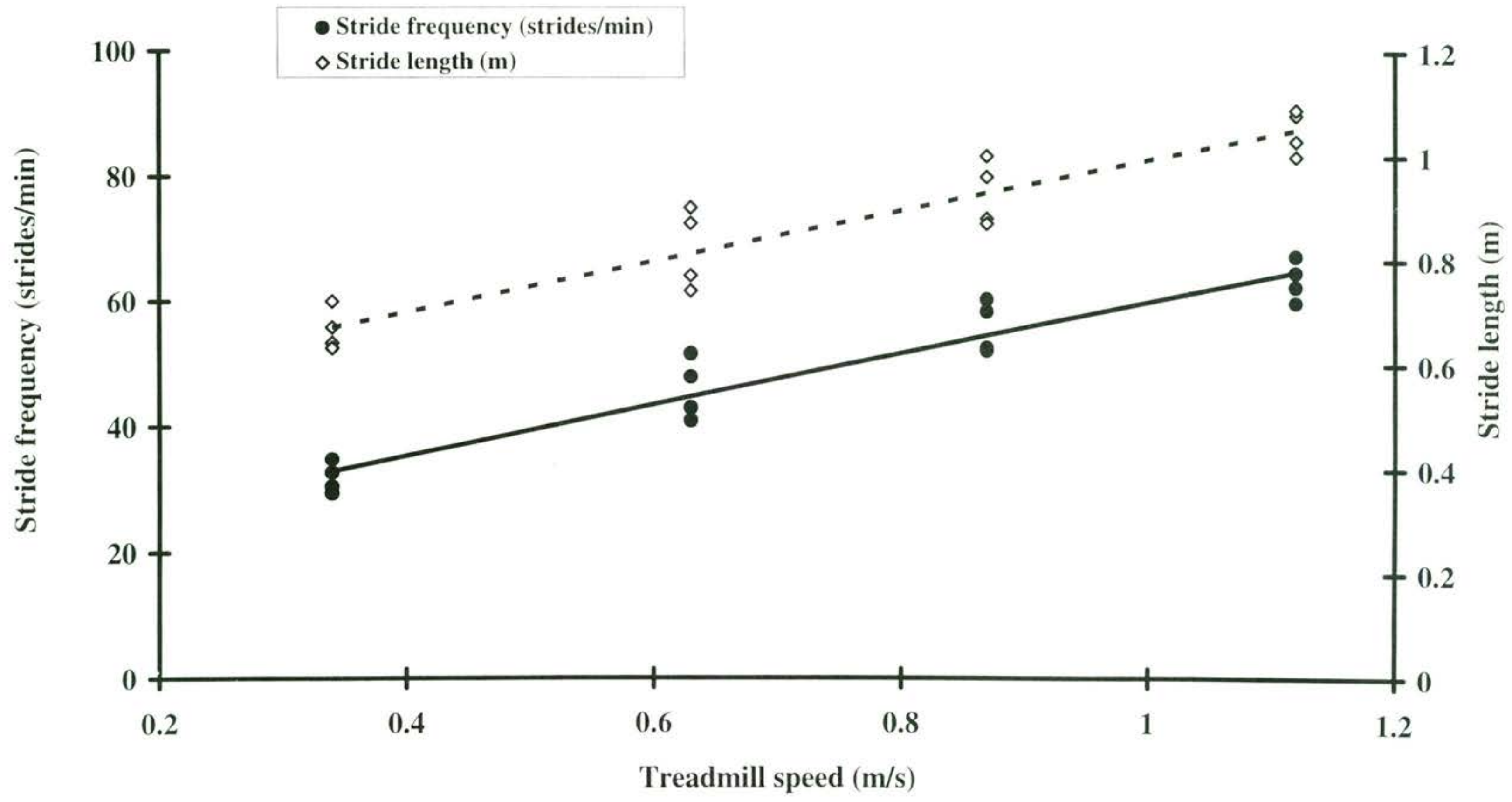


Figure 2.2b; **The relationship between treadmill speed (m/s), stride length (m) and frequency (strides/min) measured in four Shetland ponies during Period 2 of Experiment 2.1.**



Comparison between Periods 1 and 2.

Ew and TEw were each plotted against stride length and the relationship between the parameters was described by least-square linear regression. Neither Ew ($r^2 = 0.222$) nor TEw ($r^2 = 0.0002$) were related to stride length, therefore data on the energy costs of locomotion from Periods 1 and 2 were analysed as one data set.

The relationship between stride length and walking speed probably differed because the random allocation of speed in Period 1 resulted in an unpredictable environment for the ponies, whereas the treadmill speed remained the same for 6 consequtive sessions in Period 2 and was, therefore, predicatable.

2.3.8.2 Energy costs

The effect of walking speed on TEw was highly significant ($P<0.001$; GLM ANOVA) whilst the differences in SMR and Ew were not significant (Appendix 2.5). The significance of the differences in TEw between speeds was investigated using SSRs (Table 2.4).

Table 2.4; The net energy requirement (Ew) and total energy requirement (TEw) of Shetland ponies for walking on a level treadmill at four different speeds.

Speed category	*(m/s) mean (s.e.)*	*Number of animals*	*Number of measurements*	*TEw (W/kg) mean (s.e.)*	*Ew (J/kg/m) mean (s.e.)*
1	**0.34 (0.004)**	**4**	**24**	**1.67^{a}(0.03)**	**1.04 (0.032)**
2	**0.63 (0.003)**	**4**	**24**	**2.08^{b}(0.05)**	**1.05 (0.026)**
3	**0.87 (0.006)**	**4**	**24**	**2.16^{b}(0.05)**	**0.97 (0.024)**
4	**1.12 (0.007)**	**4**	**24**	**2.57^{c}(0.04)**	**1.03 (0.038)**

Within column different superscripts indicate significant differences (SSR; $P<0.05$)

The data are in Appendix 2.4.

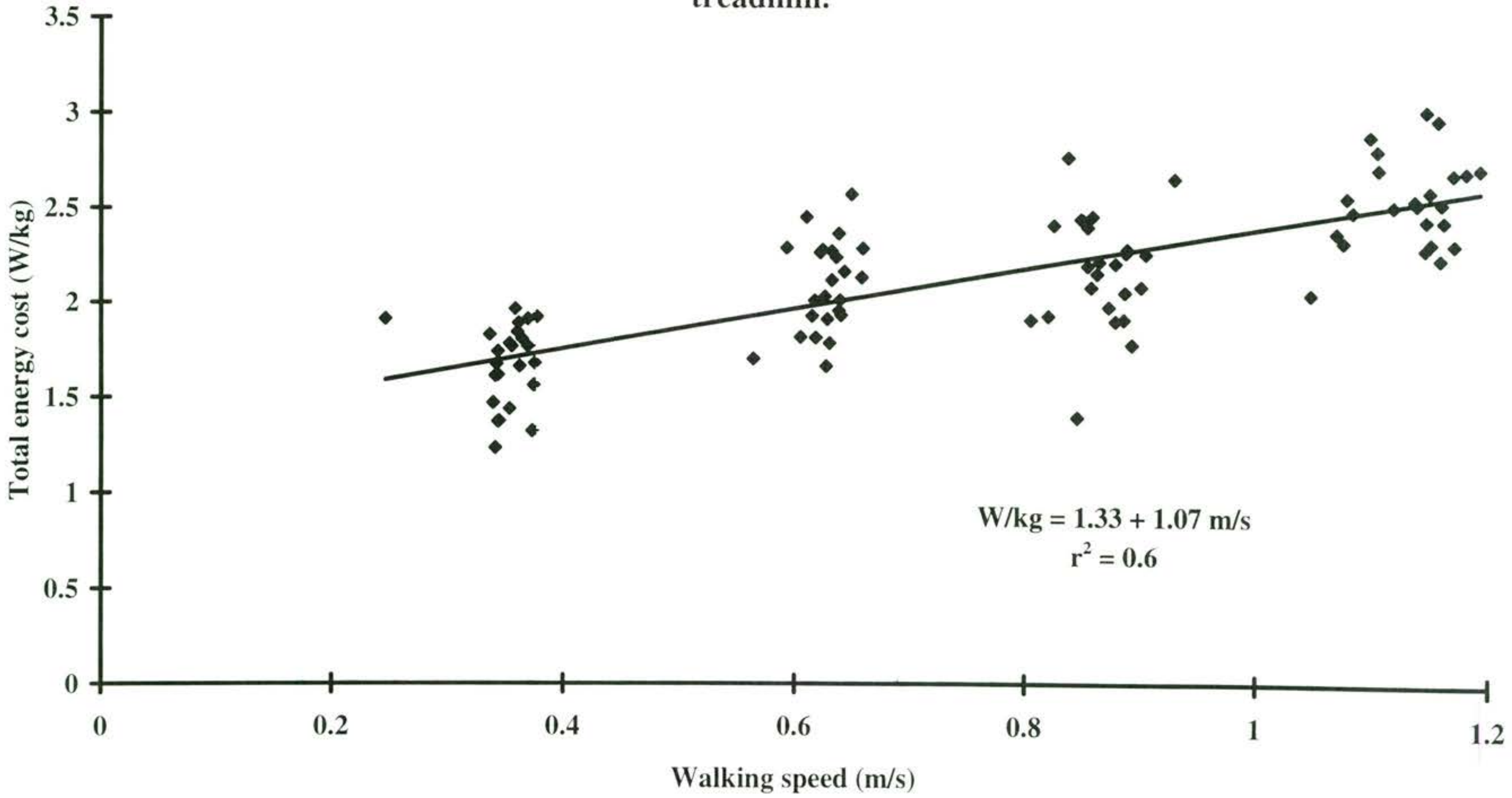
Mean Ew = 1.03 (s.e. 0.015) (n = 96).

TEw (Figure 2.3) increased significantly with speed ($P<0.001$) although TEw at speed 2 (0.63 m/s) and speed 3 (0.86 m/s) were not significantly different from each other ($P>0.05$). The relationship between TEw (n=96) and speed was described by a least-squares regression (Minitab 9.2; 1995) according to the equation:-

$$\text{TEw (W/kg)} = 1.33 + 1.07 \text{ speed (m/s)} \qquad (r^2 = 0.60)$$

The mean (s.e.) SMR (n = 96) was 1.37 (0.02) W/kg. This was higher than the value predicted by the intercept of the regression equation derived from TEw (above) which was 1.33 W/kg.

Figure 2.3; The relationship between speed of walking (m/s) and the total energy cost of walking (TEw, W/kg) as measured in four Shetland ponies walking on a level treadmill.



There was a highly significant effect ($P<0.001$) of animals on SMR, TEw and Ew although the interactions were not significant (Appendix 2.5). This indicated that the effect of speed on these variables was consistent for all of the ponies, but the values for each animal may have been significantly different. Therefore, for SMR, TEw and Ew, a comparison (SSR) was made between the means for each animal (Table 2.5).

Table 2.5; The mean (s.e.) energy costs for each of four Shetland ponies standing SMR (W/kg), and walking (TEw (W/kg) and Ew (J/kg/m)) on a level treadmill.

Animal	*Number of measurements*	*SMR (W/kg) mean (s.e.)*	*TEw (W/kg) mean (s.e.)*	*Ew (J/kg/m) mean (s.e.)*
1	**24**	**1.49^a (0.044)**	**2.23^a (0.074)**	**1.00^a (0.029)**
2	**24**	**1.48^a (0.037)**	**2.30^a (0.082)**	**1.10^a (0.031)**
3	**24**	**1.43^a (0.032)**	**2.11^b (0.065)**	**0.91^b (0.021)**
4	**24**	**1.06^b (0.024)**	**1.86^c (0.079)**	**1.09^a (0.026)**

Within column different superscripts indicate significant differences (SSR; $P<0.05$)

A curvilinear relationship was apparent for each animal when TEw was expressed as ml O_2 consumed / m travelled (ml O_2/m) and plotted against speed of walking (Figure 2.4). The polynomial equations which described this relationship for each animal were:-

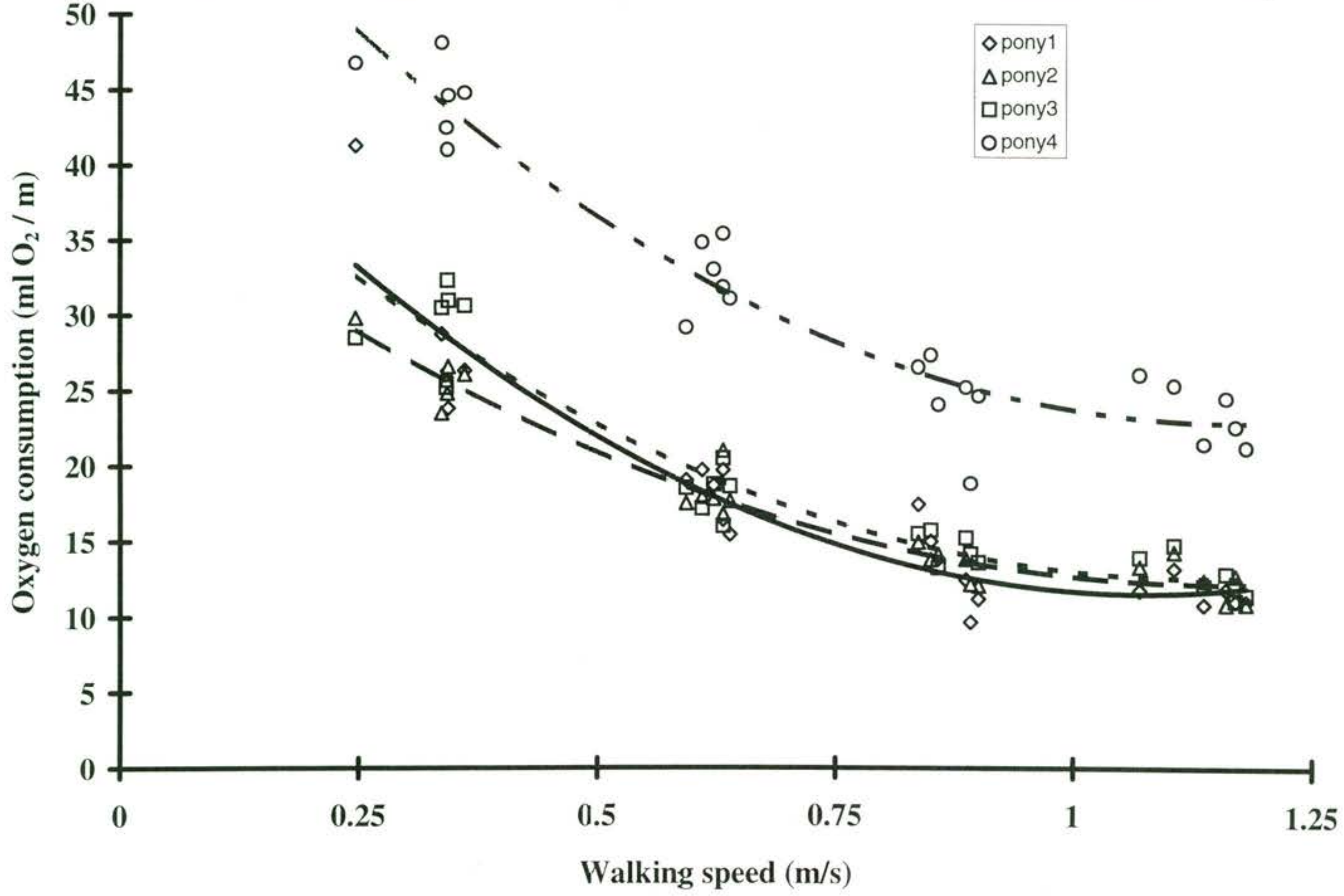
Animal No. 1 $y = 30.7x^2 - 67.1x + 48.2$ $r^2 = 0.78$
No. 2 $y = 24.3x^2 - 53.6x + 41.9$ $r^2 = 0.92$
No. 3 $y = 33.7x^2 - 71.2x + 50.2$ $r^2 = 0.93$
No. 4 $y = 41.0x^2 - 88.5x + 70.9$ $r^2 = 0.93$

The nadir of each curve represented the speed of walking at which the rate of O_2 consumption was lowest. These values are displayed in Table 2.6.

Table 2.6; The speed of walking at which the rate of oxygen consumption (ml O_2/m travelled) was lowest, according to a polynomial regression, for four Shetland ponies walking on a treadmill at a range of speeds.

Animal	*Number of measurements*	*Nadir of rate of oxygen consumption (ml O_2/m travelled)*	*Speed (m/s)*
1	**24**	**11.49**	**1.09**
2	**24**	**12.24**	**1.11**
3	**24**	**12.59**	**1.06**
4	**24**	**23.09**	**1.08**

Figure 2.4; The relationship between the speed of walking on a treadmill (m/s) and the rate of oxygen consumption (ml O_2/m travelled) in four Shetland ponies.



2.3.9 RESULTS FOR EXMOOR PONIES

2.3.9.1 Stride parameters

The stride lengths were 1.24 m for pony No.5 and 1.30 m for pony No.6. Stride frequency for these ponies was 47 and 50.4 strides/min respectively.

2.3.9.2 Energy costs

The total energy expenditure whilst walking (TEw), Ew and speed of walking differed significantly between the ponies (Table 2.7). SMR was not significantly different ($P>0.05$). The full data set is in Appendix 2.6.

Table 2.7; The total energy for standing (SMR) and walking (TEw) and the net energy for walking (Ew) of two Exmoor ponies at measured speeds.

Animal	*Speed m/s mean (s.e.)*	*SMR W/kg mean (s.e.)*	*TEw W/kg mean (s.e.)*	*Ew J/kg/m mean (s.e.)*
5	**0.88 (0.02)**	**1.39 (0.01)**	**2.03^{a} (0.12)**	**0.73^{c} (0.04)**
6	**0.94 (0.01)**	**1.41 (0.07)**	**2.46^{b} (0.16)**	**1.12^{d} (0.10)**

Figures within column with different superscripts differed significantly; a/b $P<0.05$, c/d $P<0.01$ (ANOVA).

2.4 EXPERIMENT 2.2. THE ENERGY COSTS OF STANDING AND OF WALKING ON DIFFERENT TERRAIN IN SHETLAND PONIES.

2.4.1 INTRODUCTION

There are no published reports of the energy requirements of ponies for walking on different ground surfaces or natural gradients. As these are the usual ground surfaces, not only for free-living horses but also for horses used in agriculture and sport, it is important to investigate the effects of different ground surfaces on the energy expenditure of horses in comparison to the data available from treadmill measurements.

Therefore, the following experiment was designed to measure the energy costs, for Shetland ponies, of walking on three different horizontal surfaces; concrete, grass (pasture) and mud; and of walking up and down a hill. Heart rate has been used as an indicator of energy expenditure in exercising horses. To investigate whether heart rate was a good indicator of energy expenditure under the conditions of this study, it was measured concurrently with energy expenditure in the Shetland ponies.

2.4.2 MATERIALS AND METHODS

2.4.2.1 ANIMALS AND THEIR MANAGEMENT

The five Shetland ponies used in this experiment are described in Table 2.8. Management of the animals varied. They were housed during the mud measurements and managed as detailed in Experiment 2.1. The ponies' heels were greased with vasoline® before they walked in the mud to protect them against any adverse effects of mud and water.

During the concrete and grass measurements the animals were kept at pasture with constant access to water and a salt lick. When measurements were made on a hill the animals were kept at pasture and two animals were taken at any one time and transported a few miles to the experimental site. There they were housed and fed hay at night, but turned onto pasture for three hours each morning. Pony No.3 was not used in the hill study because he had breathing problems related to local grain-drying activity.

Table 2.8; Details of the animals used in Experiment 2.2*.

Animal	*Age (years)*	*Sex*	*Height (cm)*	*Weight (kg)*
1	**3-4**	**Stallion**	**92.5**	**155-160**
2	**3-4**	"	**87.5**	**160-180**
3	**3-4**	"	**92.5**	**180-200**
8	**8-9**	**Gelding**	**95.0**	**180-200**
9	**4-5**	"	**100.0**	**220-230**

* The experiment extended over 1 year therefore a range of age and weight is given for each animal.

2.4.2.2 GROUND SURFACES

Concrete:- The path of the circular race was as described in Experiment 2.1.

Mud:- The concrete path covered with a layer of clay loam top-soil (assessed according to Silsoe Research Institute, 1992) from which stones were removed and to which water was added to create a layer of mud to reach above the fetlocks of the ponies. The mean (s.e.) depth of the mud was 12.4 (0.40) cm (Plate 2.2).

Grass:- The field where the ponies were pastured was used as the grassy surface (Plate 2.3). It was close-grazed (~1.5 cm) and the soil was dry and firm.

Hill:- A straight route through a hillside pasture (Plate 2.4) was used as the location for walking up and down hill. It was surveyed in detail using a RDS tacheometer (Department of Geology, University of Edinburgh). The surface distance of the route was 498.4 m with a vertical ascent of 50.1 m and the average gradient was 5.8° (s.e. 0.47). Sward height, mean (s.e.) 13.46 (0.63) cm, was measured using an H.F.R.O. sward stick (Bircham, 1981; supplied by Scottish Centre of Agricultural Engineering, Midlothian, U.K.).

2.4.3 MEASUREMENTS AND EQUIPMENT

2.4.3.1 RATE OF OXYGEN CONSUMPTION

An "Oxylog" (P.K. Morgan Ltd., Kent, U.K.), a portable breath-by-breath O_2 analyser, was modified for use with ponies by constructing suitable air-tight face masks, and flow meters with sufficient range (20-350 *l*/min) to measure the ventilatory volume of exercising ponies. Details of mask and flow meter construction, and the method of flow meter calibration, were as given by Dijkman (1989).

The total weight of the Oxylog equipment, 8 kg, was less than 5% of the bodyweight of the ponies used, therefore it was assumed that the energy cost of carrying this equipment would not affect the energy costs of standing or walking significantly (Pagan and Hintz, 1986b). Before field experiments began, this assumption was tested experimentally and found to be true (Appendix 2.7).

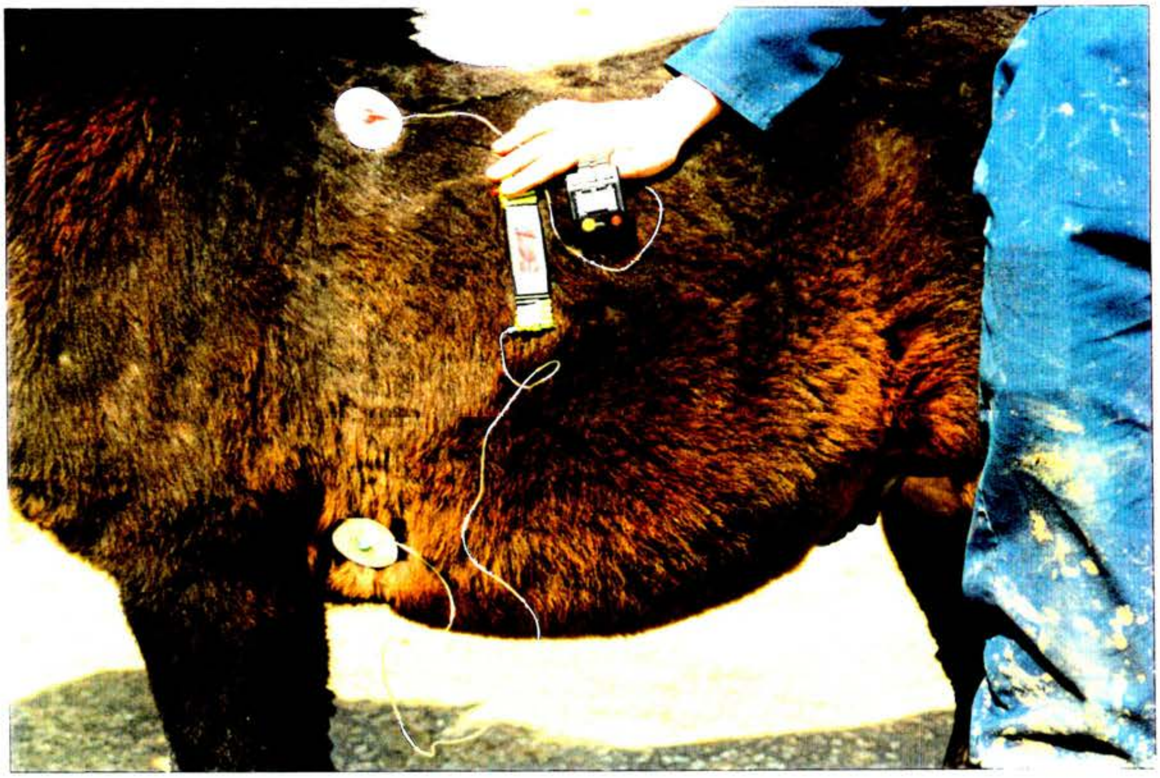
The Oxylog gave values of both minute and cumulative VO_2 (STPD) and ventilation volume (STP, 50% humidity). Because it was very difficult, during field-work, to read these data from the display panel on the Oxylog the information was transmitted to a hand-held data-display box via the Oxylog data output port.

Plate 2.2; A Shetland pony being led round the mud-filled circular race whilst carrying an Oxylog and wearing a closed face-mask. The data viewer and distance wheel were secured to the draught bar which was pushed by a second person who also recorded data using a dictaphone.

Plate 2.3; A Shetland pony being led around a marked circuit on a close-grazed pasture. The pony is carrying the Oxylog and wearing a closed face-mask. A second person carries the data viewer and uses the dictaphone.

Plate 2.4; A Shetland pony being led up hill whilst carrying the Oxylog and wearing a closed face-mask.

Plate 2.5; A Polar-Electro heart rate monitor in position on a Shetland pony. The ECG electrodes (white discs) were wired to the transmitter which emitted signals recorded by the watch-receiver.



This information was recorded on audio tape using a hand-held dictaphone and later transcribed to disc. The equipment was made waterproof to light rain by using clear plastic over the instrument dial and air-sampling tube. The filter covering the mask flow-meter was protected from rain with a "hat" made of folded rubber, and from mud with a re-modelled plastic plant pot.

Traps were built into the exhalent hose, connecting the mask to the Oxylog, to prevent condensation running back into the outlet valves of the face-mask (Figure 2.5). Vaseline® was used to seal the inside angle between the rubber base of the mask and its wooden shell to prevent condensation inside the mask from breaking the airtight seal which had been made using double sided sticky-tape and secured with electricians tape.

2.4.3.2 SPEED OF WALKING

Mud and concrete:- A programmable bicycle speedometer (Cycle Computer BC 600, Sigma Sport, Germany) was fitted to a mechanical distance wheel which was attached to the outer end of the draught bar on the circular race. The total distance, elapsed time and average speed were calculated by the speedometer and displayed at the end of each walking session. A correction factor was calculated for the difference between the distance walked by the pony around the race on each circuit and the distance travelled by the distance wheel.

Grass:- A rectangular walking track was marked out each day and the length of the path taken by the ponies round the circuit was measured three times using a mechanical distance wheel. The total number of circuits completed during the walking session was multiplied by the average distance round the circuit (~85 m) and the resulting figure divided by the time spent walking to give the walking speed (m/s).

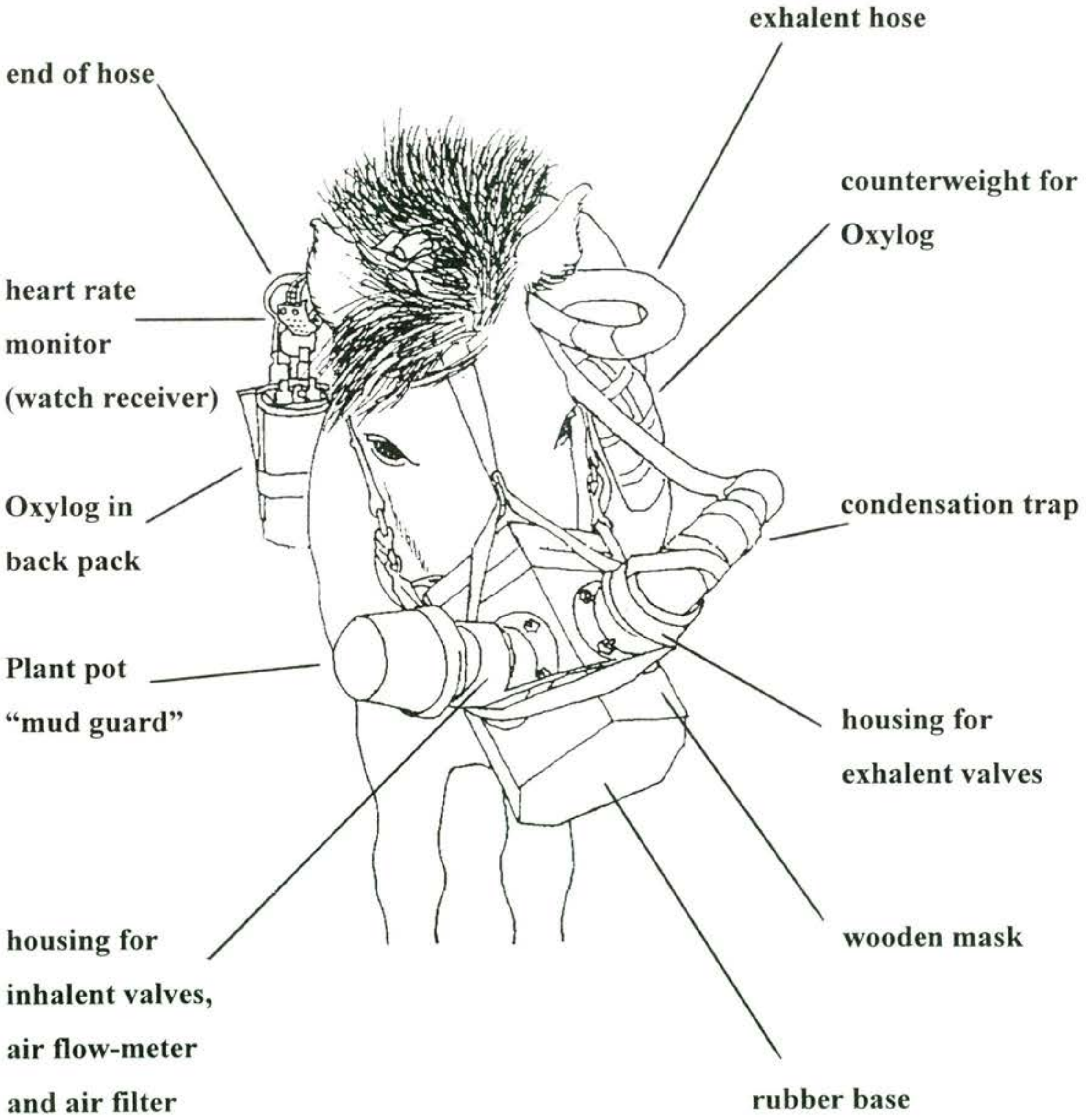


Figure 2.5; **Shetland pony equipped for the mud experiment with an Oxylog, face-mask and heart rate monitor.**

Hill:- The route on the hill was marked at 10 evenly spaced points (~50 m) whilst it was being surveyed. The distance between each marker was accurately known and the elapsed journey time was noted at each marker, therefore speed of walking was calculated as the average speed of the 11 stages of the uphill or downhill journeys.

2.4.3.3 STRIDE LENGTH AND FREQUENCY

Stride length was calculated once for each pony on each level surface. The total number of times one particular foot was placed on the ground was counted whilst the pony was walking. The elapsed time during counting (s) was divided by the speed of walking (m/s) to give the distance travelled (m), which was then divided by the number of strides to give stride length (m). Stride frequency (strides/min) was calculated by multiplying walking speed (m/s) by 60 and dividing the result by stride length (m).

2.4.3.4 TRAINING

The ponies were trained daily over a period of 3 weeks to carry an Oxylog plus its counterweight and the associated harness (6.13 kg). This included a wooden face mask (1.87 kg; Dijkman, 1993) with an airtight rubber cuff which fitted firmly around the face (Figure 2.5). All the ponies resented the mask initially but, by the end of the training period, all accepted the equipment when either standing quietly or walking (Plates 2.2 and 2.3). The animals were also trained to walk around the circular race (Experiment 2.1).

2.4.3.5 MEASUREMENT OF HEART RATE.

Heart rate (beats per minute; bpm) was recorded each minute during all field experiments. A Polar Sport Tester Heart Monitor (Polar Electro OY, Kempele, Finland;), comprising a transmitter and a data logging monitor, was used in conjunction with pre-gelled, adhesive ECG pads (Skintact F60; H.A. West X-ray Ltd, U.K.) as the electrodes. The electrodes were placed on the left side of the ponies below an elastic surcingle. One was behind the wither, 7 cm from the spine, and the other was on the rib cage level with the elbow (Plate 2.5). To ensure that a constant contact was maintained between the skin and the electrodes the hair was clipped from these sites, and the skin was dampened, before the electrodes were attached.

The transmitter and monitor were attached together to the equipment carried by the pony, and the wires from the electrodes to the transmitter were secured to prevent accidental removal. The monitor was programmed to record the average heart rate each minute and store each set of measurements on a separate file. These were later transcribed by hand or downloaded using the Polar Heart Rate Analysis Software designed for this equipment.

2.4.3.6 PROTOCOLS

Horizontal surfaces:- Animals stood or walked on mud, concrete or grass whilst their total energy cost of standing (SMR) and their total energy cost of walking (TEw) were determined. Measurements of O_2 consumption and heart rate were made whilst the pony:-

- stood for at least 20 min,
- walked for at least 20 min.

One handler led the pony while a second recorded all measurements and either pushed the draught bar behind the pony (Plate 2.2) or carried the data-viewer (Plate 2.4). Measurements of O_2 consumption and heart rate were recorded for the entire 40+ min period, but only those recorded after a steady state metabolic rate had been reached, usually after 2 min of walking, were used for calculation of energy expenditure.

Each animal completed six protocols (sessions) on every surface with the exception of ponies No. 2 and 3 which completed five sessions on mud. Ponies were only used for one session per day. All sessions were completed by all ponies on the mud surface first, then the concrete and finally the grass.

Hill:- Animals stood or walked whilst their total energy cost of standing (SMR) and their total energy cost of walking (TEw) were determined.
Measurements were made whilst the pony :-

- stood for at least 20 min,
- walked on the level,
- walked to the top of the hill route,
- walked down the hill without pausing at the top.

A total of 19 measurements were collected, four for pony No. 1 and five each for ponies No. 2, 8 and 9.

2.4.3.7 CALCULATIONS OF ENERGY EXPENDITURE

The rate of energy expenditure (SMR and TEw) was derived from VO_2 (*l*/min). The following equation was used (P.K. Morgan Ltd.):-

$$\text{energy expenditure (watts)} = [\{5 \times 4.184 (VO_2)\} \times 1000]/60$$

Corrections in VO_2 were made according to the graph of ambient temperature and relative humidity (RH) provided by the supplier (P.K. Morgan Ltd.). A stable respiratory quotient (RQ) of 1.0 was assumed, based on data collected during Experiment 2.1; RQ = 1.09 (s.e. 0.008)(n = 152).

Horizontal surfaces:- Values for SMR (W/kg), TEw (W/kg) and Ew (J/kg/m) were calculated as in Experiment 2.1.

Hill:- SMR was calculated as above. However, because the gradient of the hill varied, TEw was calculated as the mean energy expenditure for walking uphill or downhill. Ew (J/kg/m) was calculated as previously and designated $Ew_{surface}$, uphill and downhill.

Energy expenditure was also expressed as $Ew_{vertical}$ (J/kg/m ascended or descended) which was calculated as, for example, (TEw uphill - TEw level) / (bodyweight x vertical speed). Vertical speed (m/s) = vertical height of the route (50.1 m) / time taken to ascend or descend the route (s); TEw = watts; bodyweight = kg.

2.4.4 DATA HANDLING AND STATISTICAL ANALYSIS

Measurements of energy costs (SMR, TEw and Ew), walking speed (m/s), stride length (m), and stride frequency (strides/min) were compared, between surfaces, by subjecting the data to an ANOVA (Minitab 9.2, 1995). Significant differences were identified by using Tukey's pairwise comparisons ($P \leq 0.05$).

2.4.5 RESULTS

The net energy cost of locomotion, Ew (J/kg/m) differed significantly between surfaces ($P < 0.05$); grass < concrete and downhill < mud and uphill (Table 2.9; data in Appendix 2.8).

The mean (s.e.) $Ew_{vertical}$ was significantly greater for ascent 18.39 J/kg/m (3.50) than for descent -0.17 J/kg/m (3.74) ($P < 0.001$). The data are in Appendix 2.9. The mean (s.e.) speeds of vertical ascent and descent were 0.102 (0.0015) and 0.113 (0.0016) m/s respectively ($P < 0.001$).

Stride length (m) increased significantly from grass to concrete to mud ($P < 0.05$) whereas stride frequency (strides/min) was least on mud ($P < 0.05$) but not significantly different on concrete and grass (Table 2.10).

Table 2.9; The mean (s.e.) walking speed (m/s) and energy costs for five Shetland ponies standing (SMR) and walking (TEw and Ew) on grass, concrete, mud, uphill and downhill ($\pm$ 5.8^{o}).

Surface (season)*	*Number of Animals*	*Number of measurements*	*Walking speed (m/s) mean (s.e.)*	*SMR (W/kg) mean (s.e.)*	*TEw (W/kg) mean (s.e.)*	*Ew (J/kg/m) mean (s.e.)*
grass (summer)	**5**	**30**	**1.10^{a} (0.022)**	**1.17^{a} (0.037)**	**3.03^{a} (0.085)**	**1.70^{a} (0.065)**
concrete (summer)	**5**	**30**	**1.19^{b} (0.008)**	**1.58^{b} (0.082)**	**5.04^{b} (0.255)**	**2.88^{b} (0.149)**
mud (spring)	**5**	**28**	**1.00^{c} (0.011)**	**1.19^{a} (0.055)**	**6.93^{c} (0.272)**	**5.85^{c} (0.209)**
uphill (summer)	**4**	**19**	**1.02^{c} (0.015)**	**1.02^{a} (0.047)**	**6.63^{c} (0.359)**	**5.50^{c} (0.306)**
downhill (summer)	**4**	**19**	**1.13^{a} (0.016)**	**1.02^{a} (0.047)**	**4.70^{b} (0.275)**	**3.27^{b} (0.234)**

Within columns, different superscripts indicate significant differences ($P<0.05$; ANOVA with Tukey's pairwise comparisons)

* Season = time of year when the measurements were made.

Table 2.10; The mean (s.e.) stride length (m) and frequency (strides/min) of five Shetland ponies walking on grass, concrete and mud.

Surface	***Number of animals***	***Number of measurements***	***Stride length (m) mean (s.e.)***	***Stride frequency (strides/min) mean (s.e.)***
grass	**5**	**5**	**1.00^{a} (0.048)**	**66.4^{a} (2.17)**
concrete	**5**	**5**	**1.13^{b} (0.037)**	**63.1^{a} (2.51)**
mud	**5**	**5**	**1.35^{c} (0.606)**	**52.3^{b} (1.42)**

Within columns, different superscripts indicate significant differences ($P<0.05$; ANOVA with Tukey's pairwise comparisons)

2.5 THE RELATIONSHIP BETWEEN HEART RATE AND NET ENERGY EXPENDITURE (E_w) OF SHETLAND PONIES WALKING OVER DIFFERENT TERRAIN

Heart rate (bpm) was measured concurrently with energy costs in all the replicates described above. The additional energy cost of walking above standing requirements (Ew, J/kg/m), for all ground surfaces, was correlated with the relative heart rate of walking (RHR = (walking bpm)/(standing bpm); Appendix 2.10). The correlation coefficient of Ew and RHR = 0.71 (n=118). A least squares regression of Ew on RHR was described by the equation:-

$$\text{Ew (J/kg/m)} = -2.92 + 3.94\ \text{RHR} \qquad r^2 = 0.50\ \text{(Figure 2.6)}$$

The relationship between Ew and RHR in individual animals (Figure 2.7) was determined by correlation and regression of data from each animal (Table 2.11).

Table 2.11; The relationship between the additional energy required for locomotion (Ew, J/kg/m) and the relative heart rate during locomotion (RHR= walk HR/ stand HR) in five Shetland ponies.

Animal	*Measurements*	*Correlation coefficient (r) Ew:RHR*	*Coefficient of determination (r^2) Ew:RHR*
1	**25**	**0.85**	**0.71**
2	**23**	**0.75**	**0.54**
3	**15**	**0.67**	**0.40**
8	**28**	**0.90**	**0.80**
9	**27**	**0.74**	**0.53**

Figure 2.6; **The relationship between relative heart rate (work HR / stand HR) and the net energy required for locomotion (Ew, J/kg/m) using data from five Shetland ponies (n=118).**

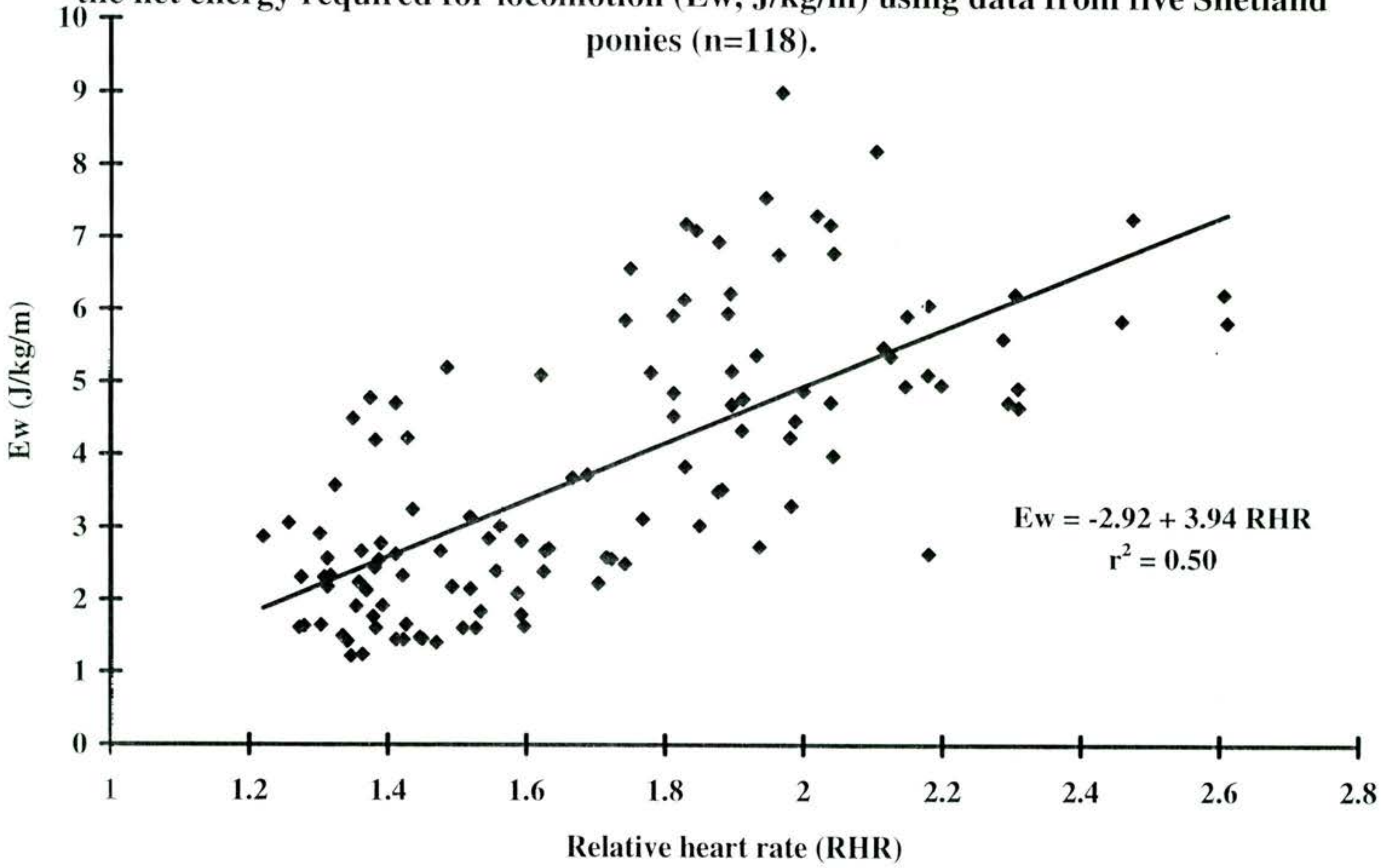
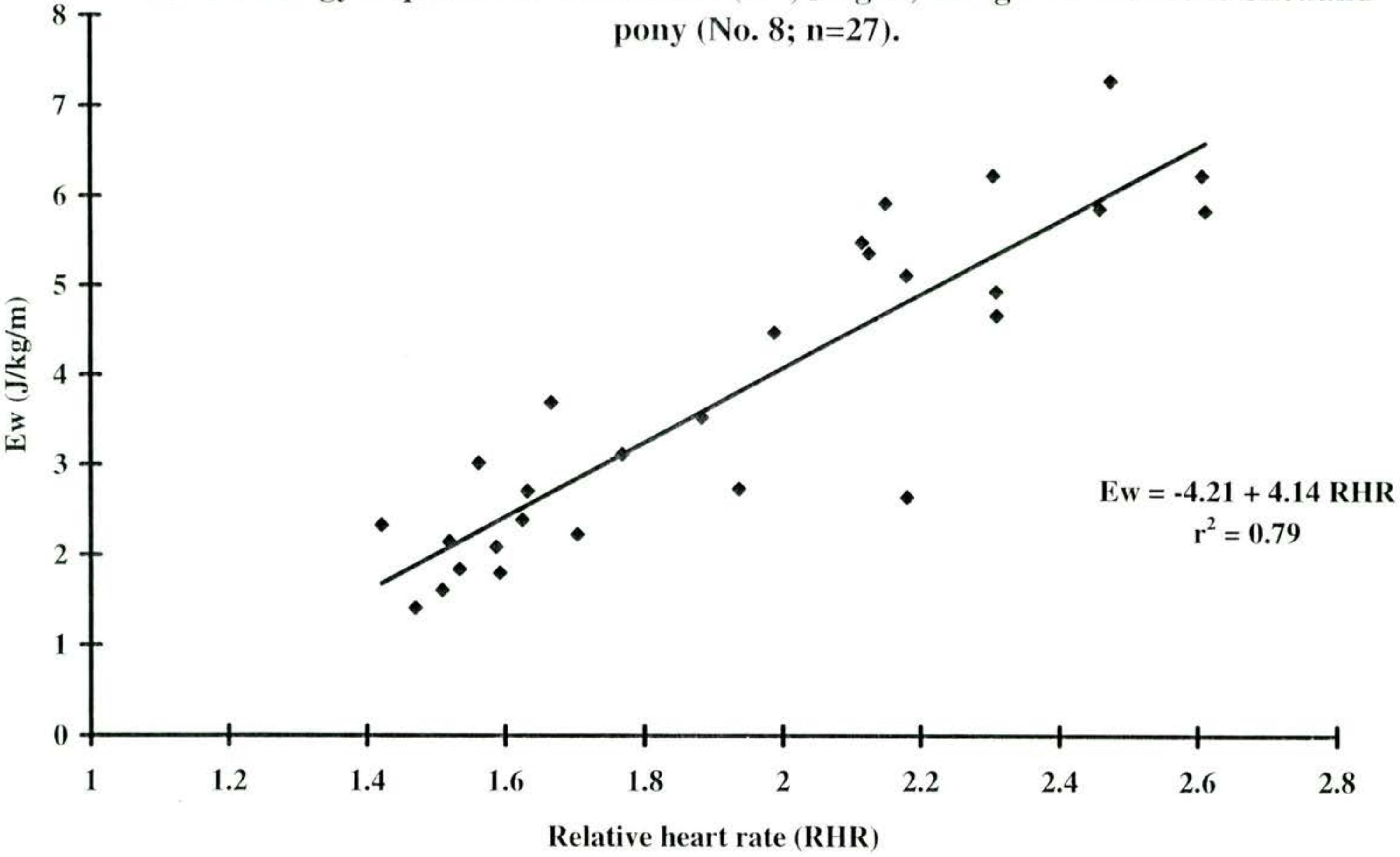


Figure 2.7; The relationship between relative heart rate (work HR / stand HR) and the net energy required for locomotion (Ew, J/kg/m) using data from one Shetland pony (No. 8; n=27).



2.6 COMPARISON OF THE ENERGY REQUIREMENTS FOR WALKING ON A TREADMILL WITH WALKING ON DIFFERENT GROUND SURFACES

The values of Ew (J/kg/m) calculated from measurements made whilst Shetland ponies walked on the treadmill at normal speed (~1.12 m/s; Experiment 2.1) were compared to Ew calculated for ponies walking on concrete, grass and mud (Experiment 2.2; ANOVA with Tukey's pairwise comparisons). Ew was significantly different (*P*<0.05) between surfaces; treadmill < grass < concrete < mud (Table 2.12).

Table 2.12; The mean (s.e.) speed (m/s) and net energy cost of walking (Ew, J/kg/m) in five Shetland ponies walking on a horizontal treadmill, grass, concrete and mud.

Surface	*Number of animals*	*Number of measurements*	*walking speed (m/s) mean (s.e.)*	*Ew (J/kg/m) mean (s.e.)*
treadmill	**4**	**24**	**1.12^a (0.007)**	**1.03^a (0.038)**
grass	**5**	**30**	**1.10^a (0.022)**	**1.70^b (0.065)**
concrete	**5**	**30**	**1.19^b (0.008)**	**2.88^c (0.149)**
mud	**5**	**28**	**1.00^c (0.011)**	**5.85^d (0.209)**

Within column, different superscripts indicate significant differences (*P*<0.05; ANOVA with Tukey's pairwise comparisons).

Stride length and frequency on the grass and treadmill surfaces were not significantly different (Table 2.13). Mean stride length on both surfaces was shorter than that on concrete, and strides were longest on mud. Stride frequency was lower on mud than on the other three surfaces.

Table 2.13; The mean (s.e.) stride length (m) and frequency (strides/min) of Shetland ponies walking on a level treadmill, grass, concrete and mud.

Surface	*Number of animals*	*Number of measurements*	*Stride length (m) mean (s.e.)*	*Stride frequency (strides/min) mean (s.e.)*
treadmill	**4**	**4***	**1.05^{a} (0.021)**	**63.6^{a} (1.60)**
grass	**5**	**5**	**1.00^{a} (0.048)**	**66.4^{a} (2.17)**
concrete	**5**	**5**	**1.13^{b} (0.037)**	**63.1^{a} (2.51)**
mud	**5**	**5**	**1.35^{c} (0.606)**	**52.3^{b} (1.42)**

Within columns, different superscripts indicate significant differences ($P<0.05$; ANOVA with Tukey's pairwise comparisons)

* Experiment 1, Period 2, 1.12 m/s.

2.7 DISCUSSION

The mean SMR for the Shetland ponies in Experiment 2.1 of this study was 1.37 (s.e. 0.02) W/kg which was within the range of 1.06 - 1.52 W/kg measured by Hall and Brody (1934), and between the values of 1.30 and 1.48 W/kg reported by Winchester (1943) and Brody (1945). When SMR was compared between the four Shetland ponies used in Experiment 2.1 (Table 2.5), pony No. 4 had a significantly lower SMR, 1.06 W/kg, than the other three ponies which ranged from 1.43 - 1.49 W/kg. The relationship persisted when SMR was calculated per kg metabolic weight ($W^{0.75}$, Poczopko, 1971; and $W^{0.87}$, Pagan and Hintz, 1986a) so was unlikely to be due to differences in body weight alone.

Another large difference between the ponies was their age. Pony No. 4 was the only mature pony (+8 years old), the others being two years old. Foals have much higher metabolic rates than adults (Ousey et al., 1991) and levels of thyroid hormones up to 10 times those in the adult (Irvine, 1984). Although these hormones decrease to adult levels by two years old (Chen and Riley, 1981) the immaturity of these animals may have contributed to the differences in SMR. Brody (1945) measured the resting metabolic rate (RMR; equivalent to SMR) of Shetland ponies from birth to 30 months but found no evidence of a change in RMR although the data set was considered to be too small to base secure conclusions on. Also, the measurements may not have continued to a great enough age because a different relationship between RMR and liveweight was found in Percheron horses after 24 months of age. However, these changes were not abrupt and had mostly occurred before 10 months of age (Brody, 1945), and appear to remain constant into old age (~22 years; McKeever and Malinowski, 1997), so would be unlikely to account for the differences seen in this study.

Animals with different temperaments may show different metabolic rates and, according to Pagan and Hintz (1986b), this is likely to influence SMR. Of the two Exmoor ponies used in Experiment 2.1 pony No. 5, the more tractable pony, had significantly lower energy costs than pony No. 6 which was more nervous and less easy to train (Table 2.7). However, significant differences were only apparent between these ponies in the TEw and Ew values, not SMR. Values of SMR for the Exmoor ponies fell within the same range as the Shetland ponies at 1.39 and 1.41 W/kg. As the possible effects of age and temperament do not appear to explain the differences in SMR, and taking the small number of ponies into consideration with the range of SMR reported from other studies (1.06 - 1.52 W/kg) the differences in Experiment 1 were probably attributable to individual variation.

The normal walking speed, on firm, level ground, of both the Shetland (1.01 - 1.19 m/s) and Exmoor ponies (1.0 - 1.31 m/s) as measured in this study, fell within the range of normal walking speeds (1 - 1.5 m/s) described by Hoyt and Taylor (1981) for one of their ponies (140 kg body weight). The walking speed of riding horses, ~500 kg, has been reported as 1.58 m/s (Pagan and Hintz, 1986b), which is 20% faster than the Exmoor ponies. The combination of body dimensions resulting in differences in conformation, as they relate to stride length and frequency, may be of greater importance in relation to the speed at which horses of all sizes walk, than either height or body weight alone (Pennycuick, 1975; Gunn, 1983; Hildebrand, 1987).

The total cost of walking (TEw), when calculated as W/kg, increased with the walking speed of the Shetland ponies on the treadmill and was described by the linear equation:-

$$\text{TEw (W/kg)} = 1.33 + 1.07 \text{ speed(m/s)} \qquad (r^2 = 0.6)$$

The difference between the value for SMR predicted by solving this equation for zero speed (1.33 W/kg) and the measured value of SMR (1.37 W/kg), may have been due to the ponies anticipating work. Transient, but significant increases in SMR occasionally occurred if the ponies were disturbed by sudden, loud noises and were excluded from calculations of SMR.

When TEw is calculated per m travelled, it is possible to describe the most economic speeds for each gait (Hoyt and Taylor, 1981). In this study the most economic walking speeds on the treadmill were 1.06 - 1.11 m/s which agree with the preferred walking speeds of these Shetland ponies measured on firm level ground; which ranged from 1.01 - 1.19 m/s. This finding is in close agreement with that of Hoyt and Taylor (1981).

The incremental costs (Ew/m) of walking on the treadmill, above SMR, were independent of speed and had an average value of 1.03 (s.e. 0.015) J/kg/m. When Ew/m was compared between the ponies, pony No. 3 had a significantly lower value (0.91 J/kg/m) than Nos. 1, 2 and 4 (1.0, 1.1 and 1.09 J/kg/m). This serves to illustrate that even though ponies of the same breed and with similar weight and height may walk most economically at similar speeds, the actual costs will vary between individuals. Despite the physical differences between the Shetland and Exmoor ponies, the similarity of their preferred walking speeds on the ground indicated that their most economic speeds of walking on a firm level surface would be similar.

The significant differences evident between the mean Ew/m for the Shetland ponies on different level ground surfaces (Table 2.9) may be explained in relation to the different locations and their influence on the biomechanics of the ponies. Differences between the grass and concrete surfaces may be related to two different factors. On the concrete surface the ponies were constantly circling which entails work against a centrifugal force. Also, the friction between the unshod hooves and the concrete surface may have been relatively high, which may have added to the concussive effects of this surface and increased the work load on the shock absorbing support structures, thereby increasing their energy requirements.

When the Exmoor and Shetland pony Ew were compared for the concrete surface the Exmoors had significantly lower values, 0.73 and 1.12 J/kg/m, than the mean value for the five Shetlands; 2.88 J/kg/m. The reasons for this are unclear, however, the Exmoor values are very close to those for riding horses, 0.85 to 1.27 J/kg/m, working outdoors around a stone dust track (Pagan and Hintz, 1986b). These values for horses are still lower than the Ew of 1.70 J/kg/m measured from the Shetland ponies whilst they walked on firm dry pasture, which suggests that small ponies do have greater energy costs for locomotion than larger horses. This possibility is further supported by the values reported by Gonzalez (1990) for small ponies trotting up gradients (Table 2.2) which were significantly greater, both in terms of metres climbed and per m travelled, than those for ponies similar in size to the Exmoors, and for Thoroughbreds. However, thoroughbred horses walking on a treadmill had Ew of 2.03 J/kg/m (Eaton, 1994) in comparison to the Shetland pony value in this study of 1.03

J/kg/m which is the inverse of the relationship seen between the values from ground surfaces. More direct comparisons of horses greatly differing in body weight need to be made before firm conclusions can be drawn.

The mud surface was made from sticky clay-loam soil and the ponies lifted their feet above the surface of the mud at each step. The height of their steps was therefore greater than normal and they also increased the length of their strides (Table 2.10). All these factors, plus the impedance of the mud, would add to the energy costs of locomotion. The 133% increase in Ew measured in mud compared to a concrete surface was greater than for cattle (90%; Lawrence, 1987). This was probably due to the depth of the mud relative to the height of the animal walking through it. Only one pony (No. 3), realised that it was easier to walk if he stepped in his own foot prints. This would be a natural way of reducing the costs of walking through snow by following in the prints of a trail-blazing animal (Fancy and White, 1985). The advantages of this activity were negated for Pony 3 by the person following who filled in the holes behind him as he walked.

In comparison to the available data for equids walking up hills, the $Ew_{vertical}$ of 18.39 J/kg/m was closer to the costs reported for donkeys (Yousef et al., 1972) than those for horses (Table 2.2). The gradients which the ponies were walked up and down were mainly grass covered and passed through open woodland; the ground was not smooth. Their energy costs of balancing and manoeuvring on such a natural surface (3.27 J/kg/m travelled) may be the reason why their energy costs for walking downhill (-0.17 J/kg/m vertical) were not as low as would be expected from the values in Table 2.2.

In the Shetland ponies, walking speed (Table 2.12) and stride length (Table 2.13) were similar on the treadmill and on the firm ground surfaces of grass and concrete. A common factor must dictate preferred speed in both situations and this would most probably be the physical proportions of the animal, as discussed earlier.

When the Ew/m on the treadmill and on firm, level grass were compared, the net cost of walking on the treadmill (1.03 J/kg/m) was approximately 40% less than for walking on the ground (1.70 J/kg/m). Neither walking speed, stride length nor stride frequency were significantly different between the treadmill and the grass surface. The methods of collecting and analysing respiratory gases were different but were not thought to be the source of the differences seen as, in a previous comparative study of these methods, Dijkman (1993) showed a mean difference in VO_2 of $\pm1.51\%$ with no differences being greater than $\pm5\%$. Net energy costs were not significantly affected by the additional work of carrying the Oxylog equipment (Appendix 2.7) and ponies did not pull on their tethers when walking on the treadmill, which would have decreased their energy costs of locomotion.

The main reason for this difference may be that the energy costs of maintaining forward momentum on the ground are greater than on the treadmill. Indeed, it is debatable whether animals on a treadmill have forward momentum or not as, in effect, they maintain position whilst the belt moves under them (Hodgson and Rose, 1994). To a certain extent, therefore, they do not have to generate propulsive forces to maintain the momentum of the body mass as a whole. If a cantering speed of 7 m/s is assumed for the treadmill versus ground (track) comparison of Sloet van Oldruitenborgh-Oosterbaan and Barneveld (1995), the 10% increase in treadmill speed required to bring heart rate and blood lactate up to track levels translates to energy costs on the treadmill being 9% less than those on the ground (according to an equation* derived from data presented by Eaton et al., 1991).

* TEwtg (W/kg) = 2.61 speed (m/s) - 0.087

Although this trend is similar, the difference is only one quarter of that seen with the Shetland ponies in this study, therefore the differences in energy expenditure on treadmill and ground surfaces may decrease with increasing speed.

Even though horses walk differently on treadmills compared to walking on the ground, according to differences in energy costs, the most economical walking speed of the Shetland ponies in this study equated with their preferred speed. On this basis it cannot be assumed that a horse will be walking normally on a treadmill, according to either energetic or biomechanical parameters, even if the walking speeds used on the treadmill are those which have been measured as the preferred walking speed of that animal on the ground. From indirect evidence of HR and plasma lactate (Sloet van Oldruitenborgh-Oosterbaan and Barneveld, 1995) this may also be the case for horses exercising at faster paces.

Heart rate has been suggested as a useful indicator of total energy expenditure in draught oxen most recently by Rometsch et al. (1997). Richards and Lawrence (1984) found that the use of relative heart rate (RHR) reduced inter-animal differences in cattle, a finding which was confirmed by Sneddon (1986). However, even when regressing Ew on RHR, the coefficient of determination (r^2) for all available data in this study was 0.50 (Figure 2.6). When the regression was repeated for each of the five Shetland ponies the r^2 was weaker than this for one pony (Table 2.11) but was greater than 0.7 for two ponies. This suggests that only 40% of animals may have close enough relationships between heart rate and energy costs and therefore this approach is probably not justified on the basis of these findings.

Pony No. 8 had the best correlation coefficient and coefficient of determination (Table 2.10; r^2=0.80; Figure 2.7). Therefore, in order to assess the accuracy of Ew estimated, for an individual and for a group, from RHR by using the regression equation for an individual animal, Ew estimated for pony No. 8 on the grass and mud surfaces was compared against the mean of its measured Ew (Appendix 2.10) and the mean Ew for all ponies (Table 2.9). Using RHR as a predictor of Ew overestimated measured values for the grass surface by 21% and underestimated measured values on the mud surface by 8% (Table 2.14). Richards and Lawrence (1984) discuss inaccuracies in estimation of energy costs from RHR at low energy expenditure due to elevated resting heart rates, possibly in response to excitement or anticipation of the work to come. This source of inaccuracy is less likely to affect the estimate as work intensity and heart rate increase, as seen in pony No. 8 on the mud surface.

Rometsch et al (1997) gave s.e. of the estimated mean y value (energy costs in watts) for individual cattle. When expressed as a percentage errors (p.e.) they ranged from 6.7 to 17.1% of the estimate for individual animals, and for all 10 cattle together p.e. was 14.4%. However, their estimated mean values of energy costs were not representative of the work loads experienced by their cattle, falling between the costs of walking and pulling. For pony No. 8 the mean Ew (y) value had a p.e. of 4.1% while the grass and mud Ew had p.e.s of 7.2% and 2.9% respectively. These p.e.s are for the prediction of a mean Ew value. When an actual Ew value is predicted the p.e.s increase to 36.6% for grass and 15% for mud. Therefore, even though the accuracy increased as energy expenditure increased, heart rate may not be a good indicator of energy expenditure.

Table 2.14; Net energy cost (Ew; mean ±s.e.) of walking on grass and mud for one Shetland pony (No. 8) calculated from measurements and estimated from the regression of relative heart rate on Ew, in comparison to the sample mean from five ponies.

Surface	*Data source*	*Ew (mean ±s.e.)*	*95% confidence intervals*
Grass	**Sample**[1]	**1.70 (0.065)**	**1.57 - 1.83**
	Pony 8[2]	**1.84 (0.127)**	**1.53 - 2.15**
	Regression[3]	**2.23 (0.162)**	**1.83 - 2.62**
Mud	**Sample**[1]	**5.85 (0.209)**	**5.42 - 6.28**
	Pony 8[2]	**5.89 (0.357)**	**5.02 - 6.77**
	Regression[3]	**5.44 (0.162)**	**5.04 - 5.83**

[1] Table 2.9; [2] Appendix 2.10; [3] Figure 2.7.

2.8 CONCLUSIONS

1. In Shetland ponies the total energy cost (TEw; watts / kg liveweight) of walking at speeds ranging from 0.34 to 1.12 m/s on a treadmill can be described by the equation:-

$$\text{TEw (W/kg)} = 1.33 + 1.07 \text{ speed (m/s)} \qquad (r^2 = 0.6)$$

2. For Shetland ponies, the net energy costs of locomotion on the ground appear to require 170% of the costs as measured on a treadmill at the same speed.

3. The net energy costs of locomotion on ground surfaces are significantly increased by soft surfaces and gradients, even at a walk. Calculations of the energy requirements for exercise will be seriously underestimated if the effects of ground surface conditions are not taken into account.

4. Heart rate was not an accurate indicator of the energy costs of locomotion in Shetland ponies.

CHAPTER 3

A STUDY OF THE HAIR COATS OF HORSES LIVING IN A TEMPERATE CLIMATE

3.1 INTRODUCTION

The Mountain and Moorland (M&M) pony breeds in the United Kingdom are considered to be adapted[1] to their environment on the basis of their ability to cope with seasonal changes in climate and the availability of food (Speed, 1960). The importance of the hair coat in this adaptation was highlighted by Speed (1960) who studied M&M ponies living in a moorland habitat and concluded that inheritance of an abnormal or poor coat was a factor which predisposed ponies to poor body condition and possible death from exposure or exhaustion.

The functions of the winter hair coat of Exmoor ponies have been described in general terms by Speed (1960) and Baker (1993). However, few measurements of the equine hair coat have been published and only three measurements; length of winter coat (Speed, 1960; Welsh, 1975), and coat density (Ellis, 1975), have been reported for M&M-type ponies living outdoors. Speed (1960) emphasised the importance of the insulation provided by the hair coat, but there have only been two reports of the external insulation of live horses (Young and Coote, 1973; Morgan, 1995). Tregear (1965) measured the rate of heat loss through samples of horse hide collected *post mortem*, and Bruce (1991) took similar measurements from thermal models of horses with a "hair coat" of artificial turf (*pers. com.* Bruce, 1991). Lack of data on the internal and external insulation of horses meant that Charles (1992) had to use data from cattle to estimate the lower critical temperature of stabled horses.

In view of the importance of the hair coat for survival, and the lack of published information, measurements of the structure of the hair coat of M&M ponies were made and are reported in this chapter. The main role of the winter hair coat is to reduce the

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[1] As defined by the International Commission for Thermal Physiology (Bligh and Johnson, 1973; cited by Yousef, 1985).

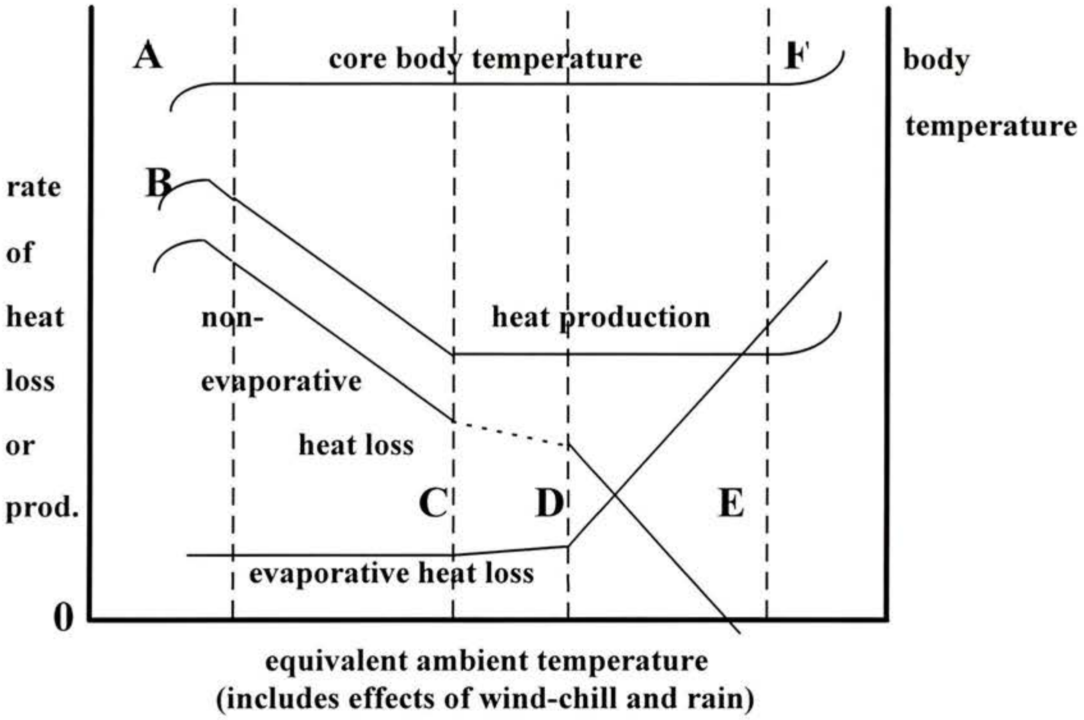
amount of body heat lost by the pony to the environment. Precipitation can significantly decrease the external insulation of cattle, therefore a study of the thermal insulation provided by the coat of Shetland ponies under both dry and wet conditions is also reported here.

3.2 LITERATURE REVIEW

3.2.1 THERMOREGULATION AND SURVIVAL

Core temperature in the adult horse is around 37.5-38 °C, whilst foals may have slightly higher body temperatures of up to 39 °C (Green, 1994). The range of environmental temperatures within which a horse makes minimal adjustments to metabolic rate or the rate of sweating is called the zone of least thermoregulatory effort, or more commonly the Thermoneutral Zone (TNZ). Definitions of the TNZ vary (NRC, 1981), but the upper and lower limits of the TNZ may be described as the upper critical temperature (UCT) and the lower critical temperature (LCT; Figure 3.1). The UCT indicates the ambient temperature above which evaporative cooling must occur to prevent core body temperature from rising. A rise of 5 °C above normal may be considered a lethal core temperature (Langlois, 1994). Below the LCT, metabolic heat production must increase to maintain body temperature. If the rise in heat production cannot be maintained then lethal hypothermia will occur (Yousef, 1985), possibly at 10 °C below normal core body temperature (Langlois, 1994).

Figure 3.1; **Thermal zones and their relationship to core body temperature and the rates of heat loss and heat production by the body.**



A	**hypothermia**	**D**	**upper critical temperature**
B	**summit metabolism**	**E**	**heat production increases**
C	**lower critical temperature**	**F**	**hyperthermia**
C-D	**thermoneutral zone (zone of least thermoregulatory effort)**		

Based on Mount (1974) and Webster (1974).

The skin and the hair coat form the thermal boundary layer across which body heat may be lost to the environment and also gained from it (Ryder, 1973). A constant internal temperature is maintained by balancing the heat generated by the normal metabolic processes of the body and the net heat lost to the environment (McArthur, 1981). The role of the winter hair coat, in maintaining a horse in the TNZ, is mainly to conserve body heat. The thicker winter coat decreases the rate of heat loss from the horse enabling it to tolerate colder climatic conditions and thereby decreasing the LCT during the coldest months of the year. Heat dissipation is more difficult through a thick coat, therefore the UCT is also decreased, consequently, the TNZ (Figure 3.1) moves to the left. The reverse occurs in the summer, the TNZ moves to the right, when the insulative value of the coat is decreased. These changes in the hair coat are an important factor in the ability of a pony to acclimatise[1] to seasonal changes in its thermal environment. Some values of UCT and LCT published for horses are displayed in Table 3.1.

Table 3.1; Summary of published values of the Lower (LCT) and Upper (UCT) critical temperature of horses in winter.

Age	*Lower critical temperature °C*	*Upper critical temperature °C*	*Feed intake*	*Exposure type/ conditions*
Foal[1] 6-9 days	13 to 23.5	~40	Suckling	Acute cold
Yearling[2]	-11	unknown	*Ad libitum*	Acclimatised
	0	unknown	Maintenance	Acclimatised
Mature[3][4]	-15	-	Restricted	Acclimatised
	-	10	Restricted	Acute cold
Mature[5]	10*	30*	not stated	Acclimatised U.K.
Mature[6]	5*	27*	not stated	U.K.

[1]Ousey *et al.*, (1991); [2]Cymbaluk and Christison (1989); [3]McBride *et al.*, (1985); [4]Young & Coote (1973); [5]Clarke (1987); [6]Sainsbury (1981).

* not supported by experimental data.

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[1] As defined by the International Commission for Thermal Physiology (Bligh and Johnson, 1973; cited by Yousef, 1985).

In the short term, a horse can alter the rate at which it loses heat to the environment in two ways. Behaviourally, a horse can move into an area sheltered from the wind, thereby raising the effective ambient temperature (EAT), by reducing wind chill, and moving EAT closer to its LCT. Non-metabolic physiological responses e.g. changes in peripheral blood-flow patterns which reduce the rate of heat loss from the surface of the body, and voluntary hypothermia (decrease in core temperature) in effect lower the LCT of the horse, bringing it closer to EAT. Voluntary hypothermia, also described as habituation (Kuhnen and Jessen, 1990, cited by Cymbaluk, 1994), has been recorded in yearling horses during daily turn-out of 5-6 hours in a Canadian winter (drop of 0.4 °C in body temperature; Cymbaluk and Christison, 1993), and in free-living Misaki horses during night time depression of ambient winter temperatures in Japan when core temperatures dropped 2 °C to 35.9 °C; Kaseda, 1983b).

3.2.2 HEAT LOSS TO THE ENVIRONMENT; RELATION TO SURFACE AREA: VOLUME RATIO AND HAIR COAT

The small surface area to volume ratio (SA:V ratio) of a large animal is of benefit in heat conservation while the opposite will facilitate heat dissipation and means that smaller horses will lose more heat than larger ones under the same conditions. Bergman's rule states that animals living closer to the poles will have larger SA:V ratios than animals of a similar type living in warm regions, and Allen's rule states that the appendages of animals living in cold regions will be smaller than those of similar animals living in warm regions because they are the areas of an animal through which large amounts of heat can be lost. Despite a report that horses from colder geographic regions have a higher compactness index (chest circumference / height at withers) and shorter extremities, in relation to horses originating in warmer regions (Langlois; 1994), detailed comparative studies have not been published therefore neither Bergman's nor Allen's rules can be confirmed or refuted for horses.

An animal'surface area is notoriously difficult to measure (Blaxter, 1989). Meeh (1879; cited by Poczopko, 1971), proposed a formula:-

$$S = kW^{2/3}$$

where S = surface area, W = body weight and k is a constant that varies depending on the general body shape of the animal.

Three methods of estimating the surface area of horses, and their associated k values, are listed by Spector (1956) with the units of measurement as:- S = cm^2, W = g. Using the minimum and maximum estimates for k; 8.2 and 10.5, the calculated surface area for a given body weight can differ by 30%. Duckett (1995) used an intermediate value of k = 10, and produced a table of the surface areas of horses of different body weights. The decrease in SA:V ratio with increasing body weight, was reflected in the the greater amount of food required to maintain body temperature during an average U.K. winter in ponies weighing 100 kg, 85 % of maintenance requirements, in comparison to those weighing 300 kg, 43 %, and horses weighing 800 kg, 11 %, (Centre for Rural Building and Aberdeen Association for the Protection of Animals, 1991).

Heat is not only lost through the body surface, but also from the respiratory tract. Horses are nasal breathers (Hayes, 1987) and the turbinate bones of the nasal passages provide a large surface area for heat exchange and are very well supplied with blood. Exercising horses have been estimated to lose 20-30 % of metabolic heat production through the respiratory system (Hodgson, McCutcheon, Byrd, Brown, Bayly, Brengelmann and Gollnick, 1993). The total evaporative heat loss of resting horses at their LCT (~ 20 ^{o}C), was 29 - 32 % of metabolic heat production (Morgan, 1995). Evaporative heat losses are thought to be minimal at LCT, and Morgan's (1995) value of 31 W/m^2 is the only one currently available for horses.

Therefore, no figures are available for the rate of heat loss from live horses in cold weather, but in cattle, respiratory losses in cold weather have been estimated to equal 10 % (Webster, 1974) and 15 % (Richards, 1973) of metabolic heat production. This heat performs the important function of warming and humidifying inspired air in the head before it reaches the sensitive tissues of the lungs. Respiratory heat loss is also an important route for heat dissipation on unusually warm winter days or after exertion because the thick winter coat reduces the effectiveness of evaporative cooling at the skin surface.

Heat loss by conduction along the fibres of the coat or through the hooves of a horse is minimal if the animal is standing. However, when an animal lies down the area in contact with the ground is increased and compression of the coat increases its conductivity. White-tailed deer have been estimated to lose 20% of heat production by conduction while lying down in both winter and summer (Jacobsen, 1980). The wetness of the ground and the physical characteristics of the ground-cover, in terms of its ability to insulate the animal from the temperature of the ground, will modify the amount of heat lost by conduction.

Heat loss by convection increases as wind speed increases. This effect, which increases as ambient temperatures decrease, is termed forced convection or wind-chill (Lloyd, 1986). Ames and Insley (1975) measured the wind-chill factors for cattle in winter and found that an ambient temperature of 0 ^{o}C could be effectively reduced to -10 ^{o}C by a wind speed of only 4.5 m/s. The effects of wind-chill on horses have not been measured. However, Cregier (1985) has observed that wind, particularly in combination with rain, can greatly increase the effects of low ambient temperatures on horses. As mentioned earlier, the extra energy above maintenance required in mild and harsh U.K. (Aberdeenshire) winters have been estimated from thermal models (MacCormack and Bruce, 1991) and published in the form of feed requirements (CRB & AAPCA, 1991). The basic structure of the winter and summer hair coats and the insulation which these coats provide under both wet and dry conditions has not been reported (Charles, 1992).

The hair coat fulfills several important roles associated with being a barrier between the horse and its external environment (Ryder, 1973; Sisson and Grossman, 1975). However, the most important role is in providing an external covering which enables the horse to regulate its core body temperature under constantly changing weather conditions (Scott, 1988).

The temperature of the skin will directly influence the temperature of the hair coat, and consequently the rate at which heat is lost through the hair coat. The rate of blood flow through the superficial capillaries varies under neural and hormonal control but can also be directly influenced by local temperature (McFarland, Pough, Cade and Heiser, 1979). Arteriovenous anastomoses are important in heat conservation because they can allow the majority of arterial blood to pass directly into the venous system without entering a surface capillary network (Scott, 1988). When this occurs the skin remains at a viable temperature by conductance of heat from sub-dermal tissues (Bligh, 1973). In the hooves, which may be in direct contact with snow or ice for long periods, cycles of vasodilation and constriction occur in the laminae during cold exposure and are thought to be important in maintaining viable hoof tissues (Pollit and Molyneaux, 1990).

Arteriovenous anastomoses occur in greatest numbers in the pinnae and the legs, areas generally exposed to the greatest effects of cooling because of their large surface area to volume ratio (Duckett, 1995) and lack of subcutaneous fat. Counter current heat exchange is also most evident in the limbs (Bligh, 1973; Palmer, 1983; Cymbaluk and Christison, 1993).

3.2.3 SEASONAL MOULTING

The coat consists of both seasonal and permanent hairs. Permanent hairs include those of the mane, forelock, tail and, in some cases the fetlocks, as well as the tactile vibrissae commonly found around the muzzle and eyes (Sisson and Grossman, 1975). Although these hairs last for longer periods than the majority of hair fibres, they are usually replaced after a year or two. The rest of the coat consists of hair fibres which grow and are moulted seasonally.

Small numbers of hairs are continuously being replaced but the co-ordinated production of the winter and summer coats is brought about by a period of active hair growth; anagen, when the new hair forces the old hair out of the follicle, followed by a period of reducing activity; catagen, and then inactivity; telogen (Blazej, Galatik, Galatik, Krul and Mladek, 1989). Moulting, therefore, principally occurs at the beginning of anagen (Ryder, 1973) although some hairs may be lost before new growth occurs (Blazej *et al.,* 1989).

Reports in the literature disagree on the number of times horses in temperate zones moult each year. Speed (1960) and Baker (1987) stated that horses moult once a year. However, Scott (1988) reported that moulting could occur in both spring and autumn. A similar discrepancy in reports on moulting in cattle was investigated by

Dowling and Nay (1960). They concluded that, in temperate climates, the summer and winter coats completely replaced each other and that the winter coat was not an elongation of the summer fibres. No such investigation has been undertaken in horses.

Change in the duration of daylight is the primary environmental factor that stimulates the seasonal patterns of moulting and coat growth (Kooistra and Ginther, 1975; Scott, 1988; Olsen, 1994). The beginning of the breeding cycle coincides with the spring moult, therefore melatonin, prolactin and other hormones associated with reproductive activity may be important in the control of moulting, as appears to be the case in other seasonally breeding mammals (Olsen, 1994). However, the level of the pineal hormone melatonin, which fluctuates on a daily and seasonal basis, increasing during darkness, is considered to be particularly important for the growth of the winter coat and its subsequent shedding (Olsen, 1994).

Temperature and nutrition have important secondary influences on coat growth and, therefore, on moulting (Yeates, Edey and Hill, 1975; Scott, 1988). Cold ambient temperatures, predominantly below 0^{o}C, have been demonstrated to delay the onset of moulting in immature horses by one month in comparison to animals housed at temperatures which did not drop below 3 ^{o}C (Cymbaluk, 1990). The effect of a low level of nutrition was shown when moulting was delayed by two to three months in New Forest weanlings fed for maintenance but not growth, in comparison to those fed for a daily liveweight gain of ~0.5 kg (Ellis, 1975). The influences of ambient temperature and level of nutrition illustrate that the onset of moulting is controlled by a number of factors and that, by delaying moulting of the winter coat in less favourable conditions, horses appear to optimise their ability to conserve body heat.

A gradual change in coat density and length occurs during moulting until the new coat is fully established. Horses moult the winter coat in a mosaic pattern (Scott, 1988). Initial moulting is over the limbs and the anterior and ventral areas of the body. The last areas to moult are the dorsal surfaces of the body (Speed, 1960). This pattern of moulting results in the thicker areas of coat forming a protective blanket for as long as possible, another method of optimising heat conservation. The pattern of moulting of the summer coat has not been described for horses.

3.2.4 THE STRUCTURE OF THE HAIRS AND THE COAT

Hair fibres consist mainly (95%) of the protein keratin (Scott, 1988). The cuticle and cortex are made of hard keratin, whilst the medulla (the core) is made of soft keratin (McFarland *et al.,* 1979) and may contain air pockets (Scott, 1988; Blazej *et al.,* 1989; Keller, 1992). In equids hair follicles are described as simple; because each one only produces one hair fibre (Scott, 1988), and the fibres are described as primary fibres because each follicle has a sweat gland opening into it (Jenkinson, 1972; Ryder, 1973; Sisson and Grossman, 1975).

The terminology and definitions used to describe fibres of different types within equid hair coats vary slightly between sources. The same fibres may be described both functionally as guard hairs (Speed, 1960), and classically as primary hairs (Ryder, 1973). For example, the term primary hair (French - jarre primaire) was translated as guard hair for the English abstract of a French paper (Keller, 1992). The term guard hair is derived from the way in which the tips of these hairs overlie, or guard, the rest of the coat (Speed, 1960). The functional description seems more appropriate in the case of the horse, as all equine coat fibres may be classed as "primary" fibres (Jenkinson, 1972).

Table 3.2; The length and diameter of guard, intermediate and fine hair fibres in the coats of *E. caballus, E. zebra and *E. przewalskii.***

Fibre type	*Guard*		*Intermediate*		*Fine*	
Species	length (mm)	diameter (μm)	length (mm)	diameter (μm)	length (mm)	diameter (μm)
E. caballus	20 - 40	60 - 95	20 - 35	35 - 60	5 - 15 (few)	10 - 25
*E. zebra**	40 - 65	80 - 130	25 - 40	50 - 80	5 - 15 (scarce)	20 - 30
E. przewalskii	20 - 35	60 - 90	20 - 35	60 - 90	5 - 15 (scarce)	10 - 15

* type of zebra undefined. Data from Blazej *et al.,* (1989).

Even though the fibres are of the same type, there is considerable variation in their length, 5 - 40 mm, and diameter, 10 - 95 μm to the extent that Blazej *et al.* (1989) distinguished between guard, intermediate and fine fibres in horses (Table 3.2), as they did in the coats of other large ungulates. However, this variation can be accounted for simply by differences in follicle size (Scott, 1988).

The differences in size between the fibres may explain why the winter coats of horses have been described as having an undercoat (Speed, 1960; Blazej *et al.,* 1989), or having two layers in comparison to the single layered summer coat (Baker, 1994). Ryder (1973) stated that fibres which form undercoats in mammals grow from secondary follicles. As, according to Jenkinson, (1972) the horse only has primary follicles it cannot have an undercoat constructed in the same way as other mammals. This view is supported by the findings of Blazej *et al.,* (1989), who reported that the undercoat of horses was indistinguishable from the rest of the coat. However, because of their variation in length; 5 to 35 mm (Table 3.2), the intermediate, and few fine fibres, probably function as an undercoat in a similar way to the shorter secondary fibres in the winter coats of animals such as deer (Blazej *et al*., 1989).

As may be expected, the density of hair follicles is greater over the more exposed areas of the body i.e. the dorsal surfaces of the neck, thorax and hindquarters (~700 - 1000 follicles/cm^2), and the lower limbs (~800 - 1200 follicles/cm^2; Watanabe, Kanemaki and Matsuura, 1993). The least density occurs over the pubic region, and the medial aspect of the upper fore and hindlimbs (~500 - 675 follicles/cm^2; Watanabe *et al.*, 1993). These values are similar to those reported by Tregear (1965) of 1290 +/- 140 fibres/cm^2 on the flank, and 850 $\pm$ 90 fibres/cm^2 on the belly.

Published measurements of coat length, depth and density (by weight and by number of hairs or follicles) are few (Table 3.3), but do indicate two general trends; 1, foals and yearlings have longer and deeper coats than mature horses under the same conditions; 2, summer coats are shorter, less dense and not as deep as winter coats.

As thin animals lose heat more rapidly than animals with an insulating layer of subcutaneous fat (Ames, 1987) it is not surprising that a trend for increasing coat length with decreasing body condition has been observed in free-living ponies (Welsh, 1975; Pollock, 1980). The association of plane of nutrition with the density (weight) of the winter coat was demonstrated by Ellis (1975) who measured a mean density of 74.4 mg/cm^2 for New Forest weanlings growing at ~0.5 kg/day, and 99.4 mg/cm^2 for weanlings kept on a maintenance diet with zero weight gain.

Table 3.3; The density, length and depth of the hair coat of horses.

	SEASON			
	WINTER		**SUMMER**	
Coat measurement	**outdoor**	**housed**	**outdoor**	**housed**
Length (mm)	**undercoat 27**[1] **40 - 100**[4]	**85**[3]		**28**[3]
Depth (mm)	**9.3 -18**[2] **20.2**[2]	**4.5**[2] **21**[3]		**2**[3]
Density (mg/cm^2)	**24 - 27**[5]	**cold heated** **40.4**[6] **27.8**[6] **37 - 39**[7] **42 - 45.6**[7] **74**[a] **- 99**[8b]	**45**[8]	**-**

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[1] Speed (1960); Exmoor pony.
[2] Young and Coote (1973); Riding horses; mature and yearling.
[3] Kooistra and Ginther (1975); Welsh/Shetland ponies.
[4] Welsh (1975); Sable Island ponies; mature and foals.
[5] McBride, Christopherson and Saure (1983); Quarter horses.
[6] Cymbaluk (1990); Standardbred foals.
[7] Cymbaluk and Christison (1993); Draught cross Quarter horse foals.
[8] Ellis (1975); New Forest weanlings. a) Average daily gain (ADG) ~ 0.5 kg. b) ADG 0.0 kg.

3.2.5 WATER-SHEDDING BY THE COAT

Individual hairs over the same body region tend to lie in the same direction as a consequence of the slope of their follicles. This creates the impression of hair streams or flows (flumina; Sisson and Grossman, 1975), also described as tracts (Ryder, 1973).

These streams meet at vortices or cowlicks (Blood and Studdart, 1988), also known as whorls (Hayes, 1987; Royal College of Veterinary Surgeons, 1984). As the coat becomes wet, small groups of hairs converge at their tips to form overlapping, elongated triangles, called tiles, that point in the direction of the hair streams (Plate 3.1). In a manner similar to roof tiles the tip of one tile overlaps the base of the next (Speed, 1960) and directs the drainage of water along the hair streams (Plates 3.2 and 3.3).

An additional factor in water shedding is the water-proofing of each hair with an emulsion of sweat and sebum. The highly polar lipids which are included in sebum are thought to be important in repelling water (Scott, 1988). The size of the sebaceous glands vary according to skin type but some of the larger ones are over the rump and dorsal surface of the neck (Scott, 1988), both important water-sheds on the horse. The amount of fat in the winter hair coat over the rump has been measured at 0.2 g/100cm^2 (Ellis, 1975).

Drainage of water off the winter and summer hair coats follows the contours of the body as well as the hair streams (Plates 3.4 and 3.5). As all breeds of *E. caballus* have the same basic pattern of hair streams, the general directions in which water drains from the coat of Exmoor ponies, as shown diagramatically by Baker (1993), are applicable to all breeds (Figure 3.2). However, the exact pattern will vary between individuals (Plate 3.5 and 3.6a) and may be overcome by long periods of continuous rain (Plate 3.6b). The pattern of water-shedding can influence the ability of a horse to tolerate extreme weather conditions if, for instance, the flank whorl is grossly misplaced and directs water onto areas of coat more susceptible to heat loss (Speed, 1960). The permanent hairs of the mane and tail are also important water-sheds. Short tail hairs, which are overlapped by hairs of the general coat at the top of the tail, act as a rain and snow chute (Baker, 1993; Plate 3.7). When the tail is blown against the hindquarters some water is directed onto the hair streams of the general coat (Plate 3.8). The protection given to the head and eyes by the forelock is evident in Plate 3.9.

Plate 3.1; **Winter coat over the costal region of a Shetland pony, anterior to the left, showing the difference between a dry coat (left side) and the tiling caused by a shower of rain. The upper area has been clipped and is dry.**

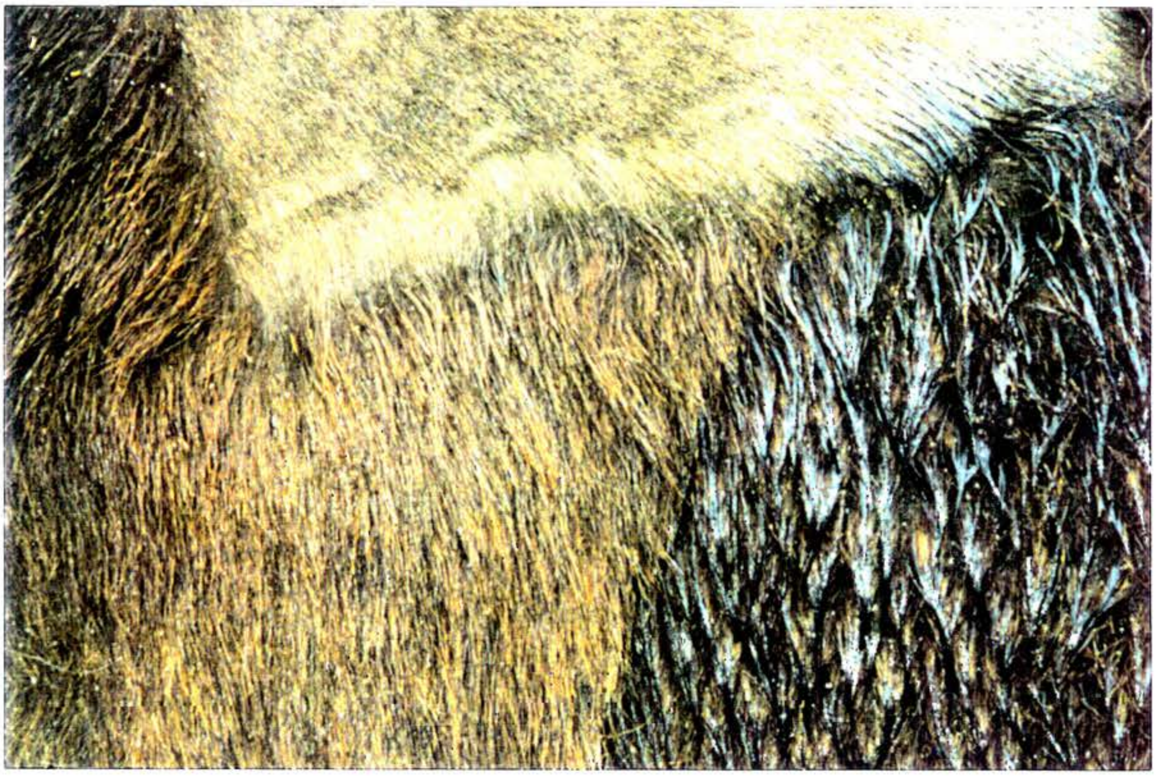


Plate 3.2; **Rain water draining past the flank and belly whorls in the summer coat of a Highland pony. Tiling is evident.**

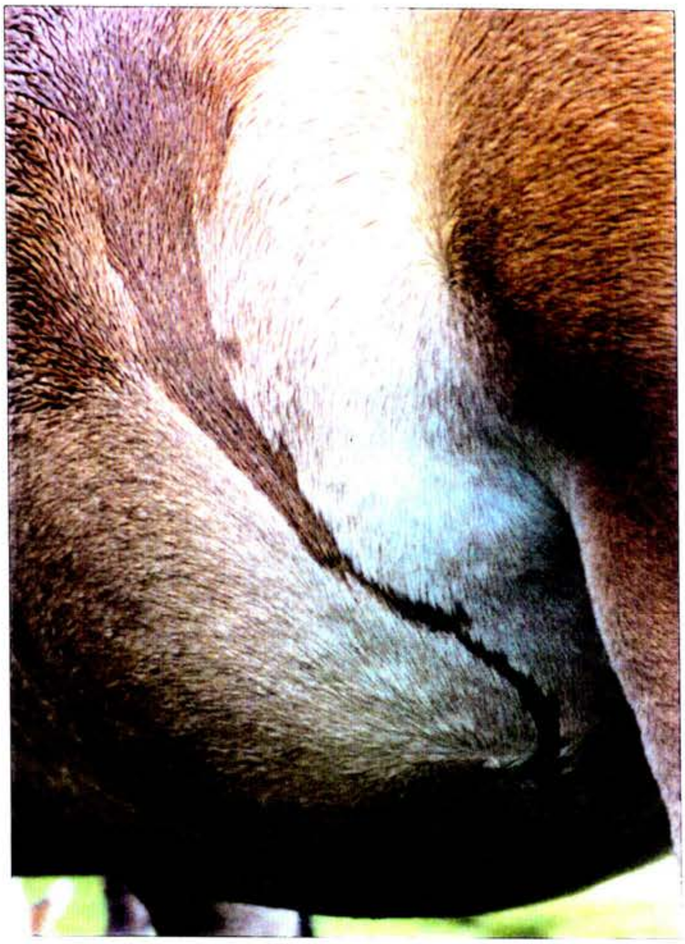


Plate 3.3; The main drainage pathways; from the croup down the back of the hind legs, and from the back and withers down the flank, are clearly shown on this light-coloured Highland pony.

Plate 3.4; **Water run-off pattern on an Exmoor pony in winter coat.**

Plate 3.5; **A very similar pattern of water run-off in the summer coat of the same Exmoor pony (above).**

Figure 3.2; **The general pattern of water run-off from the winter and summer coats of all horses (*E. caballus*).**

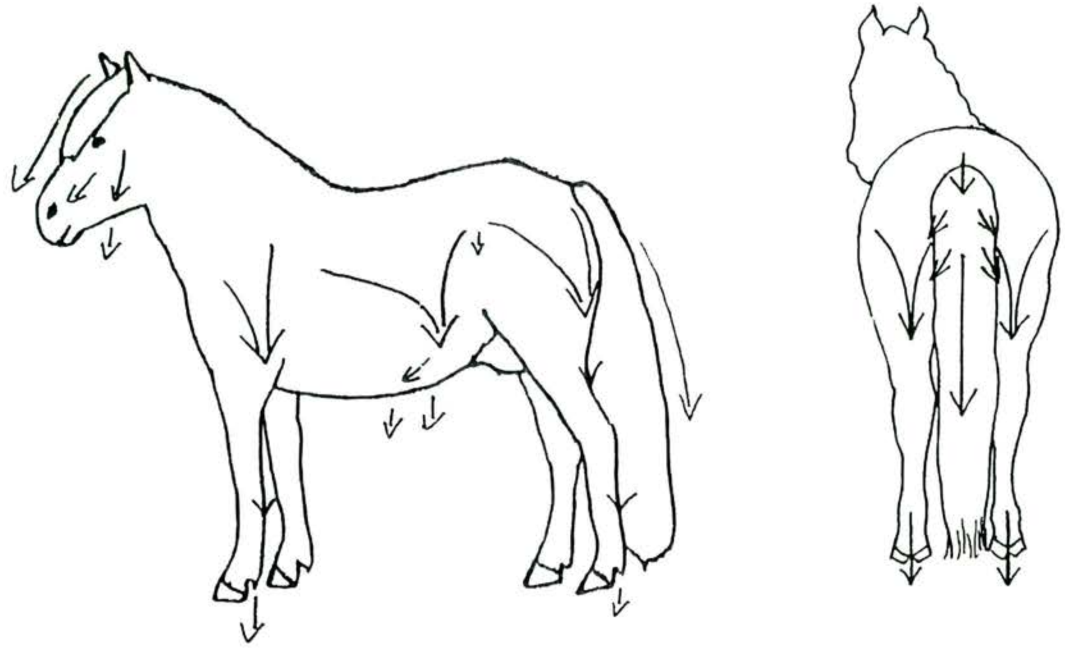


Plate 3.6a; **A light, soaking rain is draining down the flank, and the rear of the hindquarters of the summer coat of this Highland pony. Water has started to drain down the centre of the flank whorl.**

Plate 3.6b; **A Shetland pony with a saturated coat. After three days of constant rain and wind the ventral surface of the thorax and the abdomen, and the medial aspects of the limbs are heavily tiled.**

Plate 3.7; Snow/rain chute, short hairs, at the top of the tail of a Shetland pony in winter coat.

Plate 3.8; Tail of an Exmoor pony, in winter coat, spread over the hindquarters by a strong breeze.

Plate 3.9; **The face of an Exmoor pony showing the protection given to the eyes and head by the forelock.**

3.2.6 INSULATION

The body core is insulated from ambient temperature by the tissues which lie between it and the environment. When body heat needs to be conserved, the smaller the difference in temperature between the outermost surface of the body and the external environment the better. As the temperature of the body core is usually higher than that of the environment, the body core must be insulated.

Internal insulation is provided by the superficial tissues, comprising the skin and subcutaneous stores of fat. In horses the subcutaneous fat, the *panniculus adiposus* (Sissons and Grossman, 1975), is mostly stored over the dorsal trunk, hind quarters and over the ribs, the areas most exposed to wetting. Young and Coote (1973) calculated the tissue insulation of a cold-acclimated mare and yearling to be 0.421 and 0.441 $^{o}C.m^{2}.W$ respectively at a temperature of -20 ^{o}C in a climate chamber.

External insulation is provided by the hair coat. Air is an important component of this insulation as it is a poor conductor of heat. Air trapped both within and between the fibres of the coat increases the thermal resistance of the coat and thereby reduces the rate at which heat passes through it. The ability of the coat to trap air is related to the total depth of the coat (McArthur, 1981) and its density (fibres/cm^{2}) (Tregear, 1965). Piloerection increases the depth of the air column by increasing coat depth. In horses piloerection only occurs in response to cold, not fear or aggression (Goody, 1983). Young and Coote (1973) measured an increase of 4.6 mm (34%) in the coat depth of a mare due to piloerection on moving from an ambient temperature of 5 ^{o}C to one of -7 ^{o}C.

Dandruff, possibly flakes of the inner root sheath of the hairs (Blazej *et al.*, 1989) may increase the ability of the coat to trap air (Speed, 1960). Medullated hairs i.e. those with air pockets in the core, have higher insulative values than non-medullated hairs (Scott, 1988). Blazej *et al.*, (1989) reported that all the coat hairs of zebra (species undefined) were non-medullated. This was in contrast to *E. caballus and E. przewalskii* in which most of the intermediate and guard fibres were medullated. In still air, in a climate chamber at a temperature of -20 ^{o}C, the winter hair coats of a mare and yearling, plus the air trapped in them, gave external insulation values of 0.886 and 0.644 $^{o}C.m^{2}.W$ respectively (Young and Coote, 1973).

Wind disrupts the surface of the hair coat, thereby decreasing the ability of the coat to trap air, and decreasing the contribution of the coat to total body insulation (McArthur, 1981). Temperature profiles within the hair coat of the flank and belly of horses were measured by Tregear (1965) in *post mortem* hide samples in still air and at wind speeds of 6.8 and 8.05 m/s. The effective, insulating, depths of these hair coats at these wind speeds were 13, 7 and 6 mm over the flank, and 6, 3 and 2 mm over the belly. The differences in wind penetration were probably due to the differences in fibre density. The belly had one third the density of fibres/cm^2 compared to the flank (Tregear, 1965; Table 3.3).

The effects of wind speed on the conductance of a coat are reported to be linear (Campbell, McArthur and Monteith, 1980). Christophersen (1981) measured increases of 34% in the heat production of bull calves (~330 kg liveweight; gaining at 0.5 - 0.71 kg/d) exposed to winds of 4.2 m/s at temperatures of -16 to -1 ^{o}C when their coats were dry. Within a temperature range of 0 to 10 ^{o}C at the same wind speed, heat production increased by 15% with a further 5% increase when the animals were wetted. In still air between 0 and 10 ^{o}C there was no metabolic response to wetting the coat. From these results it was estimated that, for these animals, LCT would increase by 15 to 25 ^{O}C under wet and windy winter conditions in Canada.

Similar metabolic responses to wind and rain might be expected in horses and some data on the energy required, above maintenance, to meet the heat loss associated with the effects of wind and rain (climatic energy demand, CED) have been derived by Bruce (1991). Bruce (1991) used thermal models of horses located in or outside a shelter and with or without a waterproof cover simulating a rug. The results indicate that, in the year in which the measurements were made, the maximal CED was around 122 W/m^2 of body surface and that by using an open-front shelter the CED decreased by 12 W/m^2 (CRB & AAPCA, 1991). The authors state that they assumed an average hair coat and average body condition for the design of their models although they did not give measurements for these parameters (CRB & AAPCA, 1991). However, the influence of body size on the CED, in terms of additional feed requirements, was addressed. Based on the different rate at which heat is lost from bodies with a large surface area to volume ratio, even in a mild winter an unsheltered pony of 100 kg liveweight was estimated to require 170% of its maintenance energy requirements compared to the 131% required by a 300 kg pony under the same conditions (CRB & AAPCA, 1991). Mild, average and harsh were the adjectives used to describe the range of possible winter conditions in the UK, but no figures for temperature, wind speed or rainfall were given as guidelines to these categories (CRB & AAPCA, 1991).

3.2.7 AIMS OF THIS STUDY

The hair coats of M&M ponies in the U.K. have not been described in detail, neither have their insulative values. Therefore, the aims of this study were to describe the physical differences between the summer and winter coats of Shetland ponies, and to investigate the effect of wetting the winter hair coat of Shetland ponies on their coat and tissue insulation, and their metabolic rate.

3.3 EXPERIMENT 3.1. THE PHYSICAL CHARACTERISTICS OF THE HAIR COAT OF SHETLAND PONIES IN SUMMER AND WINTER

3.3.1 INTRODUCTION

Only a few objective descriptions of the coats of M&M ponies have been published, and these were limited to the coat density of New Forest ponies. The aim of this experiment was to measure the length, depth and density of the hair coat, and the length and diameter of individual fibres in the winter and summer coats of Shetland ponies.

3.3.2 MATERIALS AND METHODS

3.3.2.1 ANIMALS AND THEIR MANAGEMENT

Measurements were made from a total of six Shetland ponies; three stallions and three geldings (Table 3.4). The ponies were kept at pasture where water and a mineral lick were constantly available. During the winter months the ponies were fed meadow grass hay to meet maintenance requirements, based on N.R.C. (1989). These ponies were not groomed.

3.3.2.2 SAMPLE SITES

The nomenclature used to describe sample sites followed that used by Goody (1983) for regions of the body-surface of horses (Figure 3.3).

3.3.2.3 COLLECTION OF HAIR SAMPLES

Samples of winter coat were taken from the back, dorsal cervical and costal regions of five Shetland ponies. Samples of summer coat were taken from the back of four Shetland ponies. The following method was used to collect hair from both summer and winter coats. Foreign material was brushed from the sample area with a body brush before clipping began. The hair was clipped against the direction of growth starting from a "parting" drawn at right angles across the lie of the coat with a comb or pencil.

The length of coat left on the animals, due to the depth of the comb-plate of the clippers (2 mm), was added to the measured lengths to give the true fibre lengths.

Self-sealing plastic sample bags, labelled with water-proof marker, were pre-weighed. One lip of the opened sample bag was held against the pony directly below the area being clipped to ensure that the complete sample was collected. Samples were air-dried, by leaving them open overnight at room temperature, before weighing.

Winter samples were taken from the left side and summer samples from the right side in order to avoid any effect that removal of the winter sample may have had on subsequent growth of the summer coat.

Table 3.4; Details of the Ponies used in Experiment 3.1.

Breed	*Pony No.*	*Sex*	*Age*	*Management*
Shetland	**1**	**stallion**	**4**	**outdoor**
	2	"	**4**	"
	3	"	**4**	"
	4	**gelding**	**8+**	"
	8	"	**8+**	"
	9	"	**5**	"

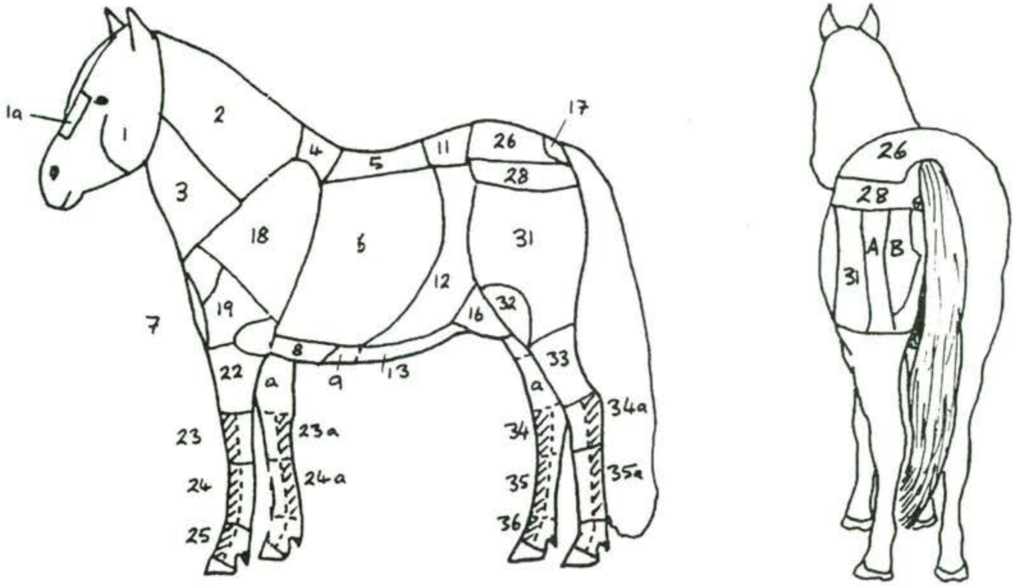
3.3.3 MEASUREMENTS

Coat *in situ* on Shetland ponies

3.3.3.1 Coat length

A ruler, the end of which was filed level with the zero marker, was used to measure coat length as follows. The hair was "parted" at right angles across the lie of the coat with a pencil (Figure 3.4). The end of the ruler was placed at the base of the lifted hair which was then repositioned over the ruler. The length of the coat was read from the ruler after the removal of loose hairs by hand. Where individual hairs were significantly longer than the majority of the coat these were measured separately and called cat hairs.

Figure 3.3; Body surface regions of the horse, as designated by Goody (1983)
The key to nomenclature is on the following page.



Key for Figure 3.3;

Nomenclature of body regions for the equidae.

Head

1. Masseteric region

1a. Dorsal nasal region

Neck

2. Dorsal cervical region

3. Ventral cervical region

Thorax

4. Interscapular region

5. Back

6. Costal region

7. Presternal region

8. Sternal region

Abdomen

9. Xiphoid region

11. Lumbar region

12. Lateral Abdominal region

13. Umbilical region

16. Pubic region

17. Tail (root of)

Forelimb

18. Scapular region

19. Brachial region

22. Antebrachial region (lateral)

22a Antebrachial region (medial)

23. Carpal region (dorsal)

23a Carpal region (palmar)

24. Metacarpal region (dorsal)

24a Metacarpal region (palmar)

25. Digit (dorsal)

Pelvis/Hindlimb

26. Sacral region

28. Gluteal region

A. Semitendinosus region

B. Semimembranosus region

31. Femoral region

32. Region of knee (lateral)

32a Region of knee (medial)

33. Crural region (lateral)

33a Crural region (medial)

34. Tarsal region (dorsal)

34a Tarsal region (plantar)

35. Metatarsal region (dorsal)

35a Metatarsal region (plantar)

36. Digit (dorsal)

Figure 3.4; **Method of measuring coat length using a ruler.**

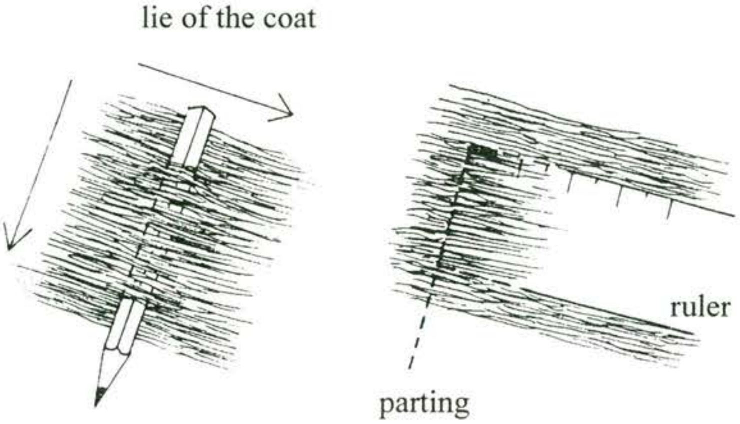
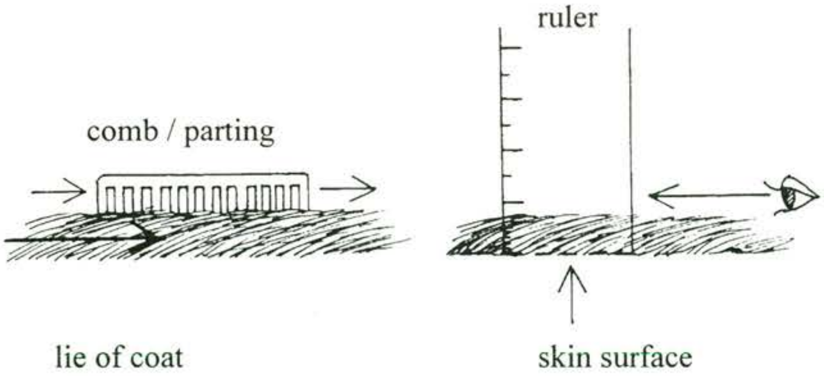


Figure 3.5; **Method of measuring coat depth using a ruler.**



3.3.3.2 Coat depth

The depth (cm) of the coat was measured by parting the hair parallel to the lie of the coat and placing the ruler at right angles to the skin with its end on the skin. Care was taken not to depress the skin as this would have given false results. A sighting was made across the coat surface and the depth read from the ruler (Figure 3.5).

Clipped coat samples

3.3.3.3 Coat density

Density (mg/cm^2) was estimated by dividing the weight of the hair sample by the area from which it had been clipped.

3.3.3.4 Fibre density

Coat density (mg/cm^2) was divided by the weight of a counted sample of 500 hairs (mg) and the resulting figure multiplied by 500 to calculate the number of hairs per unit area (fibres/cm^2).

3.3.3.5 Longest and shortest fibres

Subsamples of clipped hair were carded (method described in Appendix 3.1) so that fibres were graded according to length in such a way that measurement of the length of individual fibres was possible. The lengths (mm) of the longest and shorteset fibres in each sample were measured. The carded hair samples in Plates 3.10 and 3.11 were more densely packed, for photographic reasons, than those from which measurements were taken.

3.3.3.6 Fibre diameters

The diameters (μm), of 200 fibres per coat sample were measured at the Macaulay Animal Fibre Evaluation Laboratory, Macaulay Land Use Research Station, Aberdeen, U.K..

3.3.4 Statistical analysis

For normally distributed data, one-way analysis of variance (ANOVA) and two-sample t-tests were calculated. The Mann-Whitney test was used to compare non-parametric data. All statistical tests were computed by using the statistical package, Minitab (1994).

3.3.5 Results

Coat *in situ* on Shetland ponies

Measurements of coat length and depth were made on the two Shetland pony stallions, No. 1 and No. 3, which were also used in Experiment 3.2 (section 3.4). The measurements are summarised in Table 3.5, and listed in Appendix 3.2 (winter coat) and Appendix 3.3 (summer coat).

3.3.5.1 Coat length (*in situ*)

Winter

The longest areas of the coat were found on the palmar surface of the metacarpals and were 9.5 and 10.5 cm in length. On the thorax the longest coat was found on the lateral and ventral surfaces, maximum 5.5 cm. The coats were 3 cm long over the back, and ranged from 1.5 to 2.2 cm on the head (masseteric and dorsal nasal regions). Although the coats of the two ponies measured were similar in terms of the regions growing the longer and shorter coats, they differed in terms of the presence of cat hairs, and in the length of hair on the plantar surface of the metatarsals; 4 cm for one pony and 9.5 cm for the other.

The tails of both ponies reached below the fetlocks and covered the semimembranosus region of the hindquarters. The mane reached its maximum length in line with the point of the shoulder, while the forelock reached well down the face of both ponies.

Summer

Measurements were made in July on pony No. 1, a four year old stallion, pony No. 3 was already showing signs of shedding the summer coat so was not used. The following seasonal comparisons refer to pony No. 1 only. The summer coat on the head was similar in length to that of the winter coat. The summer hair coat in each body region was generally one third the length of the winter coat, with three exceptions:-

On the interscapular and tail root regions, coat length decreased in summer by less than half its winter length to 2.5 cm and 1.75 cm respectively. The greatest seasonal difference in length was measured on the palmar surface of the metacarpals where the winter coat was 10.5 cm and the summer coat was 1.2 cm long.

<u>Table 3.5</u>; Description of the coat length (cm) over 6 areas of the body of 2 Shetland ponies, in winter and summer.

Winter

*Body areas**	*No. of Ponies*	*No. of measurements*	*min.*	*Q1*	*median*	*Q3*	*max.*
Head[1]	**2**	**4**	**1.5**	**1.63**	**2.0**	**2.15**	**2.2**
Dorsal[2]	**2**	**12**	**3.0**	**3.5**	**3.75**	**4.0**	**4.5**
Lateral[3]	**2**	**24**	**1.5**	**3.1**	**3.75**	**4.5**	**6.0**
Ventral/[4] medial	**2**	**11**	**2.0**	**3.0**	**4.0**	**5.0**	**5.5**
Lower limbs							
Dorsal[5]	**2**	**12**	**2.0**	**2.5**	**3.0**	**3.38**	**4.0**
Palmar/[6] plantar	**2**	**8**	**2.5**	**3.12**	**5.25**	**9.5**	**10.5**

Summer

*Body areas**	*No. of Ponies*	*No. of measurements*	*min.*	*Q1*	*median*	*Q3*	*max.*
Head[1]	**1**	**2**	**1.2**	**-**	**1.5**	**-**	**1.8**
Dorsal[2]	**1**	**6**	**0.9**	**0.9**	**1.25**	**1.94**	**2.5**
Lateral[3]	**1**	**12**	**0.6**	**0.73**	**0.9**	**1.15**	**1.4**
Ventral/[4] medial	**1**	**6**	**0.2**	**0.28**	**0.35**	**0.73**	**0.8**
Lower limbs							
Dorsal[5]	**1**	**6**	**0.7**	**0.78**	**1.2**	**1.5**	**1.5**
Palmar/[6] plantar	**1**	**4**	**1.0**	**1.05**	**1.3**	**1.48**	**1.5**

*Numerical references to constituent body regions which are displayed in Figure 3.3:- **1;** 1, 1a **2;** 4, 5, 11, 17, 26, 28 **3;** 2,3, 6, 12, 18, A, B, 19, 22, 31, 32, 33 **4;** 7, 8, 9, 22a, 32a, 33a **5;** 23, 24, 25, 34, 35, 36 **6;** 23a, 24a, 34a, 35a

3.3.5.2 Coat depth

The measurements of coat depth are summarised in Table 3.6 and listed in Appendices 3.2 (winter) and 3.3 (summer).

Winter

Depth of coat in the Shetland ponies tended to be greater on the lateral aspects of the thorax than on the dorsal regions. Coat depth ranged from 4.5 to 2 cm on the body, and from 0.5 to 2.5 cm on the lower limbs. The semimembranosus region, which underlay the tail hairs, showed a reduction in coat depth, in comparison to the adjacent region (semitendinosus), of 2.3 cm and 1.3 cm in ponies No.1 and No. 3 respectively.

Table 3.6; Description of the coat depth (cm) over 6 areas of the body of 2 Shetland ponies, in winter and summer.

Winter

*Body areas**	*No. of Ponies*	*No. of measurements*	*min.*	*Q1*	*median*	*Q3*	*max.*
Head[1]	**2**	**4**	**0.5**	**0.5**	**0.5**	**1.25**	**1.5**
Dorsal[2]	**2**	**12**	**1.5**	**2.0**	**2.0**	**2.94**	**3.5**
Lateral[3]	**2**	**24**	**0.2**	**2.0**	**2.63**	**3.5**	**4.0**
Ventral/[4] medial	**2**	**11**	**1.0**	**1.5**	**2.0**	**4.0**	**4.5**
Lower limbs							
Dorsal[5]	**2**	**12**	**0.5**	**0.5**	**0.75**	**1.0**	**1.5**
Palmar/[6] plantar	**2**	**8**	**0.5**	**0.63**	**1.5**	**2.31**	**2.5**

Summer

*Body areas**	*No. of Ponies*	*No. of measurements*	*min.*	*Q1*	*median*	*Q3*	*max.*
Head[1]	**1**	**2**	**0.2**	**-**	**0.2**	**-**	**0.2**
Dorsal[2]	**1**	**6**	**0.3**	**0.3**	**0.4**	**0.53**	**0.6**
Lateral[3]	**1**	**12**	**0.2**	**0.23**	**0.3**	**0.38**	**0.5**
Ventral/[4] medial	**1**	**6**	**0.1**	**0.18**	**0.2**	**0.4**	**0.4**
Lower limbs							
Dorsal[5]	**1**	**6**	**0.4**	**0.4**	**0.45**	**0.9**	**0.9**
Palmar/[6] plantar	**1**	**4**	**0.4**	**0.43**	**0.6**	**0.85**	**0.9**

*Numerical references to constituent body regions, which are displayed in Figure 3.3:-
1;1, 1a **2;** 4, 5, 11, 17, 26, 28 **3;** 2,3, 6, 12, 18, A, B, 19, 22, 31, 32, 33 **4;** 7, 8, 9, 22a, 32a, 33a **5;** 23, 24, 25, 34, 35, 36 **6;** 23a, 24a, 34a, 35a

Summer

The results are from pony No.1 only. In this animal the coat was less than 1 cm deep over the whole body. The range for most regions was 0.2 to 0.5 cm deep, a 5-7 fold decrease in depth when compared to the winter coat. The regions with the greatest depth, 0.9 cm, were the carpal region (dorsal), metatarsal region (plantar) and the hind digit (dorsal). The crural region (medial) had the least depth of coat with 0.1 cm.

Clipped coat samples

3.3.5.3 Coat density (mg/cm^2)

There were no significant differences in mean winter coat density (Appendix 3.4a) between the dorsal cervical, 74.4 (s.e. 4.22) mg/cm^2, back, 96.2 (s.e. 8.10) mg/cm^2 and costal regions 75.3 (s.e. 10.4) mg/cm^2 (n=5, ANOVA, Minitab, 1989).

The summer coat from the back of the Shetlands, 29.5 (s.e. 3.37) mg/cm^2, was significantly less dense ($P<0.001$) than the winter coat from the same region (n=5, ANOVA, Minitab, 1989).

3.3.5.4 Fibre density (fibres/cm^2)

The mean fibre density of the back region in the summer; 925 (s.e. 136.5) was not significantly different from the winter density; 1028 (s.e. 21.5) (n=4, ANOVA, Minitab, 1989; Appendix 3.4b).

3.3.5.5 Longest and shortest fibres (mm)

Winter coat

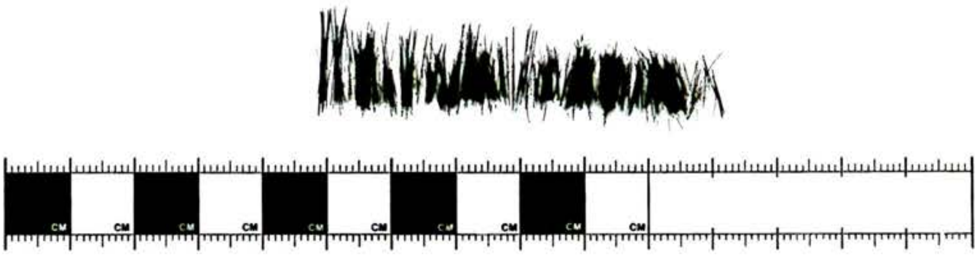
There were no significant differences in the mean (s.e.) length of the longest fibres on the back, 58.0 (19.0) mm, dorsal cervical, 63.2 (2.77) mm and costal regions, 75.0 (20.5) mm (two sample t-tests, Minitab, 1989). Although the costal region had the longest mean length, and the longest fibres for three ponies, the longest fibres for ponies 1 and 2 were from the dorsal cervical region (Appendix 3.5). Of the shortest fibres, those from the dorsal cervical region, 9.3 (1.71) mm were significantly shorter ($P<0.05$) than those from the back, 13.2 (2.77) mm, while those from the costal region, 9.6 (1.82) mm were not significantly different from either of the other two regions (two sample t-tests, Minitab, 1989).

Summer coat

The mean (s.e.) maximum and minimum fibre lengths (mm) from the back region, 17.2 (0.50) and 6.7 (0.56) mm respectively, were both significantly shorter ($P<0.005$) than in the winter coat (Plates 3.10 and 3.11; Appendix 3.6).

Plate 3.10; The range of fibre lengths in a sample of winter coat from the back region of Shetland Pony No. 2.

Plate 3.11; The range of fibre lengths in a sample of summer coat from the back region of Shetland Pony No. 2.



3.3.5.6 Fibre diameters (μm)

The fibre diameters (μm) of hair taken from the summer and winter coats from the back region of six Shetland ponies were measured from samples of 200 fibres (Table 3.7). Ponies No.1 and No.3 had significantly larger fibre diameters in the summer than in the winter (*P*<0.05, Mann-Whitney test; Figure 3.6). The fibres of greatest diameter, seen in ponies No.1 and No.4 in the winter and pony No.9 in the summer, tended to occur singly (Figure 3.7).

Table 3.7; Description of fibre diameters (μm) based on 200 fibres taken from the winter and summer hair coats of the back region of six Shetland ponies.

Winter

Pony No.	*min.*	*Q1*	*median*	*Q3*	*max.*
1*	**18.8**	**58.5**	**67.4**	**76.5**	**275.6**
2	**9.1**	**58.3**	**67.0**	**73.2**	**98.5**
3*	**12.6**	**48.0**	**56.7**	**64.3**	**117.2**
4	**20.9**	**80.3**	**90.4**	**100.1**	**242.1**
8	**14.7**	**63.3**	**76.1**	**86.0**	**114.3**
9	**20.5**	**63.2**	**73.4**	**82.7**	**99.6**

Summer

Pony No.	*min.*	*Q1*	*median*	*Q3*	*max.*
1*	**13.0**	**69.3**	**78.0**	**84.0**	**110.0**
2	**16.0**	**61.0**	**70.0**	**82.0**	**113.0**
3*	**15.0**	**46.3**	**58.0**	**67.0**	**96.0**
4	**11.0**	**69.3**	**92.5**	**103.0**	**123.0**
8	**13.0**	**56.3**	**72.0**	**88.0**	**110.0**
9	**19.0**	**58.0**	**70.5**	**89.0**	**200.0**

* summer median significantly greater (*P*<0.05) than winter median (Mann-Whitney test)

Figure 3.6; Distribution of the diameter (μm) of 200 hair fibres taken from the back of Shetland pony No. 3 in winter and summer.

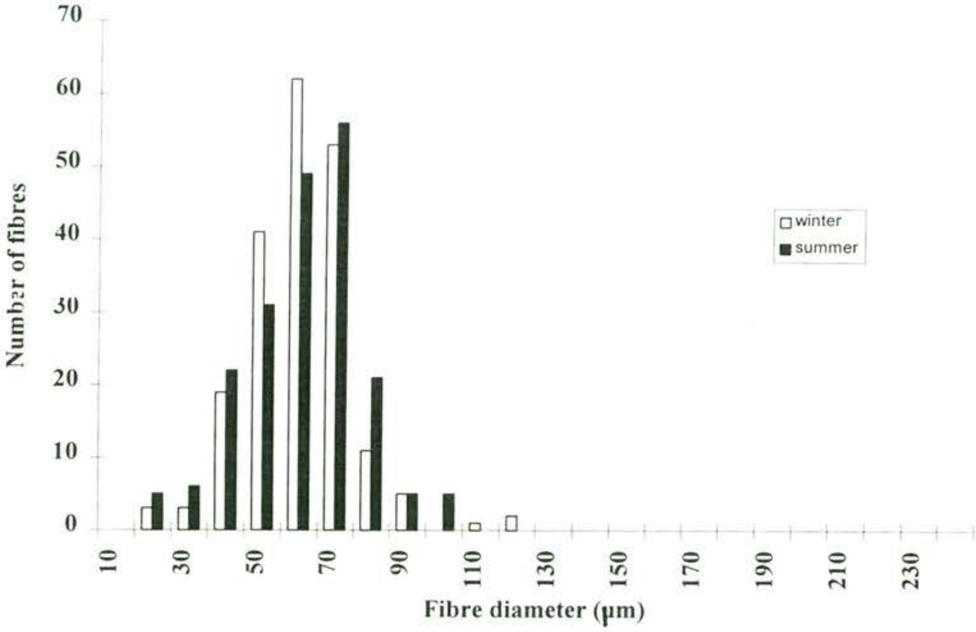
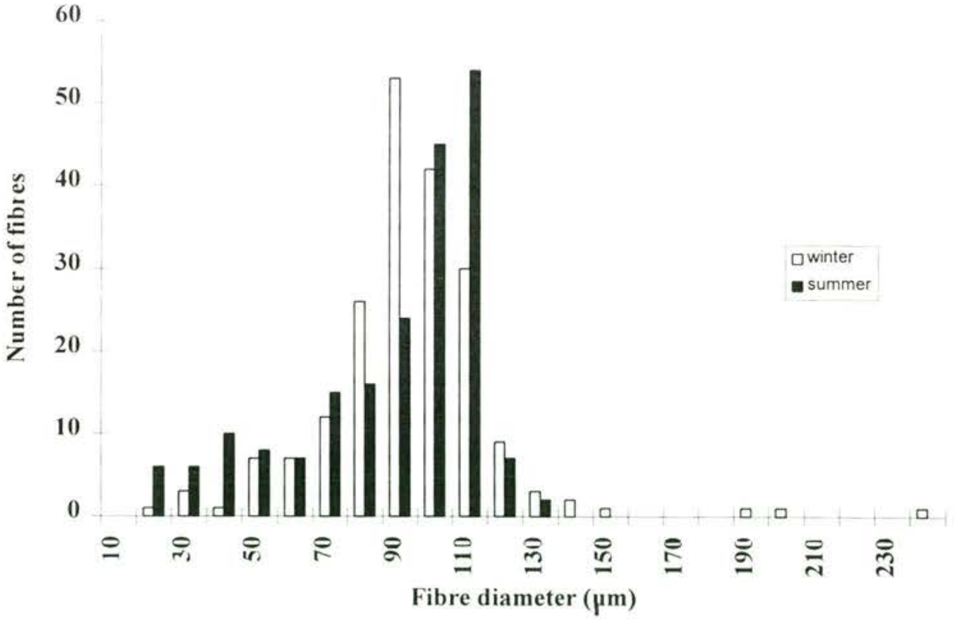


Figure 3.7; Distribution of the diameter (μm) of 200 hair fibres taken from the back of Shetland pony No. 6 in winter and summer.



3.4 EXPERIMENT 3.2. THE EFFECT OF SATURATION OF THE BACK AND RUMP OF SHETLAND PONIES IN FULL WINTER COAT ON METABOLIC RATE, RECTAL TEMPERATURE, SURFACE TEMPERATURES AND HEART RATE

3.4.1 INTRODUCTION

There are two published studies on the thermal insulation of horses' coats (Young and Coote, 1973; Morgan, 1995), but only one of these contains information for a M&M pony; a Shetland which was stabled in heated accommodation. Although the effects of cold ambient temperatures on the metabolic rate of horses has been investigated (Young and Coote, 1973; Morgan, 1995), the additional influence of wetting the coat, a common condition in temperate climates (Cregier, 1985), has not been explored. From reports in the literature that the metabolic rate of cattle increases when their coats are wet (Christopherson, 1981), this effect requires investigation in horses.

3.4.2 MATERIALS AND METHODS

Indoor laboratory facilities were available where ponies could be wetted at ambient temperature during continuous collection of respiratory gases. The back and rump were saturated with water as these areas are the natural water-shed (3.2.5). The nomenclature used in this experiment for the points of the horse were taken from Goody (1983).

3.4.2.1 ANIMALS AND THEIR MANAGEMENT

Two mature Shetland pony stallions; pony 1 and pony 3 (178 and 200 kg body weight respectively; Table 3.4) were housed in a straw-bedded pen (10.6 m x 4.5 m) in an open-sided building. The ponies were fed meadow grass hay (~ 3.5 kg / head / day), based on maintenance requirements (N.R.C., 1989), in two equal meals at 0800 h and 1600 h, and had access to water *ad libitum*. Both ponies were healthy, in good body condition (condition score 2, Pollock, 1980) and in full winter coat.

The ponies were habituated to the procedures of this experiment during a period of two weeks before data were collected. They were used alternately as the experimental subject, with the second pony as a companion.

3.4.2.2 SATURATION OF THE COAT WITH WATER

To mimic the worst possible natural conditions it was decided to completely saturate the coat. During a preliminary study it was found that when the ponies were hosed with water for 10 minutes the coat was only wetted to a depth of 1 or 2 mm. Saturation of the coat to the skin was achieved by hosing the ponies whilst brushing against the lie of the hairs with a plastic curry comb. Care was taken to ensure that the coat lay in the normal direction at the completion of the 10 min saturation. An area from the base of the tail to the point of shoulder was saturated from the midline of the back, from the withers, to hip-height on both sides.

3.4.3 MEASUREMENTS

3.4.3.1 MEASUREMENT OF RESPIRATORY GASES

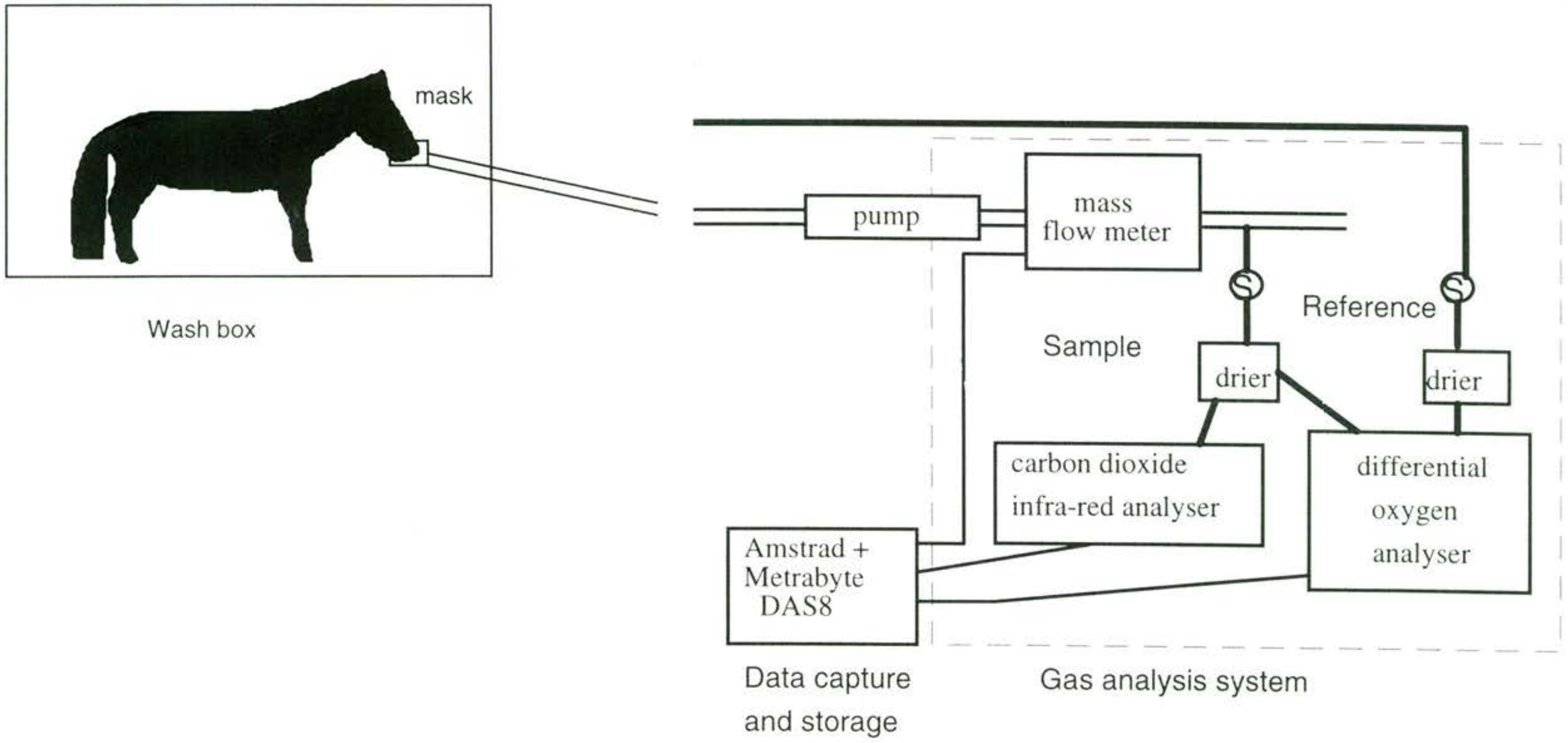
Oxygen consumption and CO_2 production were measured using an open-flow circuit, indirect calorimetric method (2.3.3.3; Figure 3.8). During measurements the ponies were tethered in a wash box (3 m x 3.3 m x 2.2 m high) next to the gas analysis laboratory. They wore a loose-fitting face mask through which exhaled gases were drawn for analysis (Plate 3.12). Reference gas samples were taken simultaneously from the wash-box, which was well ventilated.

3.4.3.2 WATER FLOW-RATE AND TEMPERATURE

Water flow-rate (WFR) was measured by timing the delivery of a known volume of water through the hose.

Water temperature (WT) was measured by suspending the probe of a water-proof digital thermometer (Pronamic, West Meters Ltd, U.K.) in the water collected while measuring flowrate.

Figure 3.8; Schematic diagram of the open-circuit gas analysis system and the wash box.



3.4.3.3 ESTIMATION OF THE WET AREA OF COAT AND THE EQUIVALENT GROUND SURFACE AREA.

The total area of wet coat was estimated from a simple set of measurements. The vertical contour distance from the midline of the spine to a point level with the hip was measured using a tape laid against the coat. Measurements were made at the withers; one perpendicular and the other to the point of the shoulder; the widest part of the rib cage, the hips and the tuber ischium. Distances between these points were also measured along the spine (Figure 3.9). All measurements were transferred to graph paper and the perimeter points joined. The resulting silhouette was enlarged x 200% using a photocopier, cut out and weighed (scales accurate to 0.1 mg) and the surface area calculated from a calibration ratio of weight : area of paper.

In order to equate the amount of water used to saturate the ponies, with rain-fall figures, the area of ground "sheltered" by the wet area of the ponies was measured as follows. The horizontal distance from the spine to the widest part of the body at hip height was measured at five places; the point of shoulder, wither, widest part of the rib cage, hip and tuber ischium. The method described above was then followed in order to calculate ground-surface area (Figure 3.10).

Figure 3.9; **Outline of the surface area of wet coat on pony No. 1 after saturation.**

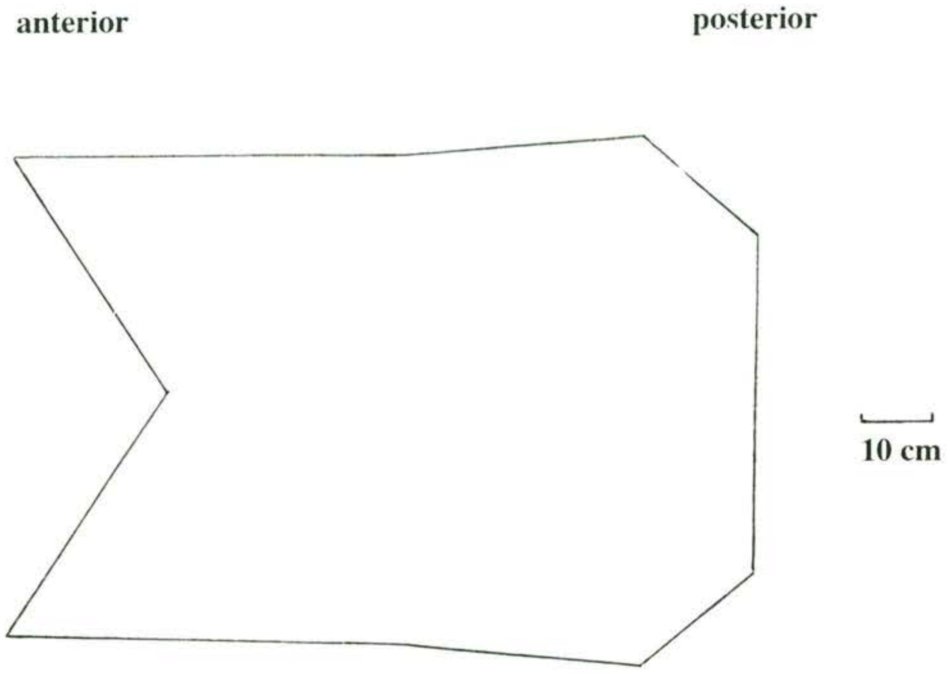


Figure 3.10; **Outline of the ground-surface area "sheltered" by the areas of pony No. 1 which were wetted.**

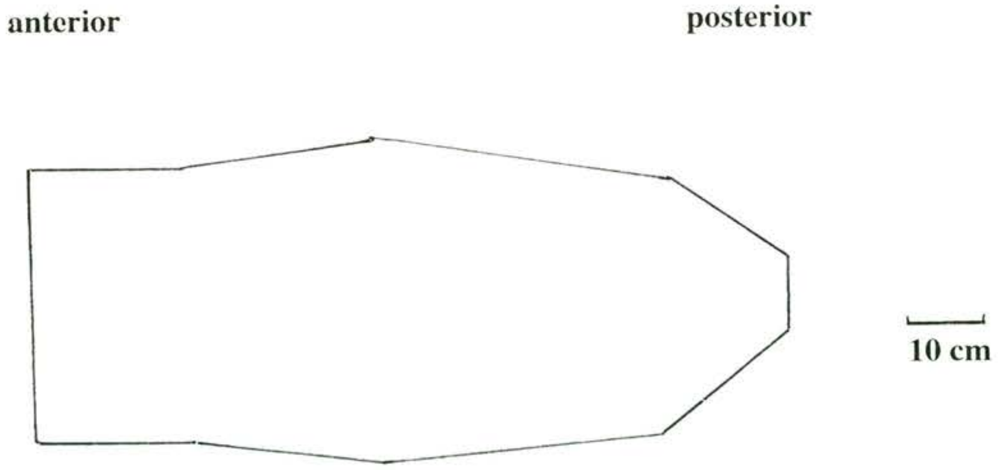


Plate 3.12; Pony No. 3, after saturation of its dorsal surface with water, and wearing a face-mask and heart rate moniter whilst standing in the wash box. The points where temperatures were measured are marked by white discs.

3.4.3.4 ATMOSPHERIC CONDITIONS

Ambient temperature ranged from -5 to +11 ^{O}C during the experimental period (maximum / minimum thermometer, G.H. Zeal, London, England).

Air temperatures for both the wash-box and the airflow into the gas analysis equipment were recorded using wet (WBT) and dry (DBT) bulb mercury-in-glass thermometers (Brannan, London, U.K.).

Relative humidity (RH%) was read from tables of DBT and depression of WBT (Brannan, London, U.K.).

Atmospheric pressure (mm Hg) was measured, using a manometer.

3.4.3.5 RECTAL AND BODY SURFACE TEMPERATURES

Rectal temperature (RT) was measured using a suitably protected thermistor (IVAC R 821, IVAC R Corporation, San Diego, U.S.A.) which was hard-wired to a LCD unit on which the temperature was displayed in ^{O}C. The rectal probe was brought to 38 ^{O}C (near body temperature) by warming in water before insertion into the rectum to approximately 15 cm.

Surface temperatures at the skin/hair (S/H) and hair/air (H/A) interfaces were measured using a touch thermometer. This instrument was constructed using a miniature bead thermistor (RS Components Ltd, U.K.) mounted on a plastic spatula and wired to a multimeter (205 Digital Multimeter, Rapid Electronics, U.K.) from which readings of resistance (ohms) were taken. The sensitive surface of the thermistor was placed against the skin for measurements at the S/H interface, and against the coat surface for measurements at the H/A interface. Temperatures were measured at three sites; neck, back, and rump (Plate 3.12). The neck was never wetted.

The calibration of all the thermometers, including the digital thermometer used to measure water temperature, is described in Appendix 3.7.

3.4.3.6 HEART RATE

Heart rate was measured using a waterproof Polar Heart Rate Monitor (Polar-electro Ltd) programmed to record heart rate automatically at frequencies of 1 min (2.4.3.5).

3.4.4 PROTOCOL:-

1. The O_2 and CO_2 analysers were calibrated (Dijkman, 1989).

2. The recording of baseline O_2 and CO_2 levels was started. Wash-room WBT and DBT were recorded.

3. The floor of the wash-room was wetted and the hose was left running outside the wash-room to allow the water temperature to stabilize. The flowrate was adjusted to approximately 8 *l*/min.

4. Both ponies were tethered in the wash-room before the heart rate monitor, rectal thermometer and face-mask were fitted to the subject. Recordings were begun, and continued for at least 20 min during which steps 5 and 6 were completed.

5. Dry coat temperatures were taken; S/H, H/A (neck, back and rump) as well as the rectal temperature. The rectal thermometer was then removed.

6. Water temperature and flowrate were measured.

7. The hair coat was saturated by hosing and brushing for 10 min. All the resulting drainage water was collected and measured.

8. Water temperature and flowrate were measured.

9. Wet coat temperatures were taken as for step 5. The rectal thermometer was reinserted and then left *in situ*. Wash-room WBT and DBT were recorded.

10. Step 9 was repeated at one hour intervals, timed from the end of step 7, until completion of the experiment (180 mins post saturation).

11. All of the equipment was removed from the subject. Final baseline recordings of O_2 and CO_2 were made.

12. The subject was rubbed down and covered with a light-weight blanket placed over a layer of straw. Both ponies were given hay and left for one hour.

13. The ponies were returned to their pen.

14. Recordings of O_2 and CO_2 were stopped and the data were saved on disk.

3.4.5 CALCULATION OF THERMAL INSULATION AND LOWER CRITICAL TEMPERATURE

The insulative value of the external hair coat and air (I_e; $^oC\ m^2\ W$), and of the body tissues, including the skin (I_t; $^oC\ m^2\ W$), were calculated using the following formulae developed for cattle (Webster, 1974):-

$$I_e = (T_s - T_a) / M - E \qquad I_t = (T_b - T_s) / M$$

where I_e = external insulation $^oC\ m^2\ W$ (hair coat and the surrounding air)

I_t = tissue insulation $^oC\ m^2\ W$ (including the skin)

T_s = skin temperature ^oC

T_a = air temperature (DBT ^oC)

T_b = rectal temperature ^oC

$E = 17\ Wm^2$ (minimal latent heat loss in cold)

M = metabolic rate (watts/m^2 of body surface area)

Body surface area (m^2) = $0.1W^{2/3}$ where W= body weight (kg)

Calculations of I_e and I_t for the ponies when dry were based on the average temperatures of the neck, back and rump (Appendix 8c-h). When the ponies were wet the calculations were made twice, firstly using measurements from the neck (always dry) and secondly using the average measurements from the wet back and rump.

Lower critical temperature (LCT; ^{o}C) was calculated according to the formula published by Webster (1974)[1] for cattle.

$$\mathrm{LCT} = (T_b + E\, I_e) - M (I_t + I_e)$$

LCT calculated for dry ponies used I_t and I_e values calculated from average surface temperatures as explained above.

When the ponies were wet, LCT was calculated firstly from values of I_e and I_t calculated for the wet surfaces which gave an LCT for 20 % of the surface area of the pony, and secondly from values of I_e and I_t for the neck and this LCT was taken to represent the remaining 80 % of the surface of the pony,. Therefore, the final LCT for wet ponies represented the whole animal, not just the wet areas, using the equation:-

$$\text{Wet Pony LCT} = (4\text{LCT neck} + \text{LCT wet})/5$$

3.4.6 RESULTS

3.4.6.1 Environmental measurements, metabolic rate, heart rate, rectal and surface temperatures

The average conditions of the experiments are described by the following measurements (mean (s.e.)):-

Air temperature	DBT 6.0 (1.15) °C WBT 3.62 (1.14) °C
Relative humidity	64.75 (3.13) mmHg
water temperature	5.26 (0.19) °C
water flow rate	7.95 (0.52) *l*/min

There were no significant changes ($P>0.05$) in metabolic rate, rectal temperature or heart rate after saturation of the hair coat (Table 3.8a). The only significant ($P<0.05$)

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[1] The formula as published contains I_a where I_e should be used according to the explanation in the text of the paper.

changes in surface temperatures were recorded from the skin of the back and rump immediately after soaking (Table 3.8b). Elevated metabolic rate and heart rate were recorded from pony No. 1 whilst he was being wetted during the first two replicates (Appendix 3.8a and c). The complete results are tabulated in Appendix 3.8a - h.

The S/H temperatures for pony No. 1, at a dry bulb air temperature of 3.5 ^{0}C during the final replicate (Appendix 3.8g), show the trends which were evident in the experiments, with temperatures at the skin surface of the wetted areas decreasing and remaining low (Figure 3.11). Temperatures at the H/A interface did not change significantly after wetting on either the rump, back or neck ($P<0.05$; paired t tests).

Figure 3.11; Temperature (°C) at the skin/hair interface of Pony No.1, on the neck, back and rump, plus the rectal temperature, before and after soaking the whole dorsal surface except the neck.

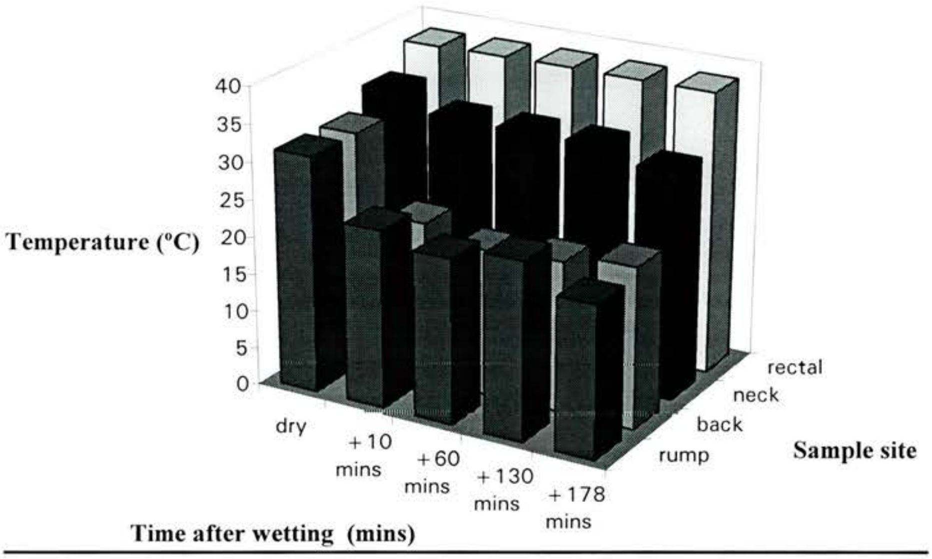


Table 3.8a; Mean (s.e.) values (n = 6) of the standing metabolic rate (SMR; W/kg), rectal temperature (^{0}C) and heart rate (b.p.m.) of two Shetland ponies in winter coat when dry, soaked with water and at 1, 2 and 3 hours after soaking.

State of the coat	*SMR (W/kg)*	*Rectal temperature (°C)*	*Heart rate (bpm)*
Dry	1.39 (0.053)	37.9 (0.03)	33.8 (0.76)
Soaked	1.45 (0.056)	37.9 (0.04)	33.9 (0.54)
+1 hr	1.34 (0.072)	37.9 (0.02)	34.4 (0.53)
+ 2 hr	1.34 (0.101)	37.8 (0.02)	34.7 (1.21)
+ 3 hr	1.36 (0.073)	37.9 (0.02)	34.9 (1.16)
significance	NS	NS	NS

Table 3.8b; Mean (s.e.) values (n = 6) of temperature (^{0}C) at the skin/hair interface, and the hair/air interface on the neck (always dry), back and rump of two Shetland ponies in winter coat when dry, soaked with water and at 1, 2 and 3 hours after soaking.

	Temperature at the skin/hair interface (^{o}C)			*Temperature at the hair/air interface (^{o}C)*		
Region of body	Neck	Back	Rump	Neck	Back	Rump
State of the coat						
Dry	32.3 (0.46)	30.6* (0.97)	30.9* (0.51)	18.6 (1.89)	18.3 (2.24)	19.8 (1.27)
Soaked	31.5 (0.80)	20.8 (0.83)	21.3 (0.94)	14.6 (1.48)	15.0 (1.00)	15.5 (0.47)
+1 hr	32.4 (0.58)	22.9 (1.27)	23.7 (1.15)	16.3 (1.68)	17.2 (1.34)	17.8 (1.33)
+ 2 hr	32.2 (0.45)	23.3 (1.11)	23.3 (1.03)	14.9 (1.98)	17.5 (0.91)	16.1 (0.47)
+ 3 hr	31.8 (0.52)	22.9 (0.08)	22.8 (1.13)	17.0 (1.57)	16.3 (1.37)	17.0 (1.53)
significance	NS	$P<0.05$	$P<0.05$	NS	NS	NS

3.4.6.2 Wet surface areas, and equivalent ground surface area

The wet surface areas of ponies No. 1 and No. 3 were 5850 cm^{2} and 6928 cm^{2} respectively. These areas represented approximately 20 % of the total surface area of the body when using the formula $S_{(\text{surface area})} = kW^{2/3}$ where k = 0.1 and W = body weight in kg.

The wetted areas covered a ground surface area of 3575 cm^{2} for Pony 1 and 3843 cm^{2} for Pony 3. Therefore, the amount of water applied to the ponies (~ 80 *l*) was equivalent to a rainfall of 188 mm in 10 minutes.

3.4.6.3 Thermal insulation

The resistance to heat loss, as represented by the calculated values of I_e and I_t, increased significantly ($P<0.05$) through the coat after wetting, but decreased through the tissues (Table 3.9 and 3.10). This resulted in a non significant ($P>0.05$) change in total insulation, $I_e + I_t$, after wetting (Table 3.10). There was a general trend for I_e and I_t, to increase as ambient temperature decreased, although the trend was more consistent for I_e compared to I_t.

Table 3.9; The mean values of tissue (I_t) and external (I_e) insulation (°C m^2 W) of the neck, back and rump measured in two dry Shetland ponies in winter coat, and values of I_t and I_e for the neck (dry) and the mean values for the back and rump 3 h after soaking with cold water (~5 °C).

Thermal insulation (°C m^2 W)

		Ambient temperature	*Dry pony*		*Partly wet pony*			
		DBT (°C)	dry neck back and rump		dry neck		wet back and rump	
Pony	Replicate		I_t	I_e	I_t	I_e	I_t	I_e
No. 1	3	9.5	0.088	0.332	0.086	0.338	0.198	0.196
	2	7	0.103	0.412	0.095	0.445	0.233	0.267
	4	3.5	0.079	0.602	0.127	0.641	0.290	0.412
No. 2	3	8	0.059	0.367	0.070	0.349	0.123	0.284
	2	6	0.095	0.336	0.066	0.357	0.165	0.234
	4	2	0.071	0.429	0.054	0.483	0.192	0.308

Table 3.10; Median (n=6) values of the external (Ie), tissue (It) and total thermal insulation (Itotal) of Shetland ponies when dry and when partly wet.

median thermal insulation (°C m^2 W)

	dry pony	*partly wet pony*	
		dry neck	**wet back and rump**
I_t	**0.084 ^{ax}**	**0.078 ^{ax}**	**0.195 ^{b}**
I_e	**0.389 ^{ay}**	**0.401 ^{ay}**	**0.276 ^{b}**
Itotal (I_t+I_e)	**0.466**	**0.519**	**0.484**

Within rows different superscripts indicate significant differences ($P<0.05$; Mann-Whitney test)

Within columns different superscripts indicate significant differences between It and Ie ($P<0.05$).

Lower Critical Temperature

The estimated values for LCT are presented in Table 3.11. The calculated LCT was very close to the ambient temperature of the experiment in all cases.

Table 3.11; The estimated lower critical temperature (LCT °C) of two Shetland ponies when dry and when partly wet 3 h after being soaked over the back and rump with cold water.

		ambient temperature	*LCT (°C)*	
Pony	**Replicate**	**(°C)**	**dry pony**	**partly wet pony**
No.1	**2**	**7**	**7.02**	**7.12**
	3	**9.5**	**9.30**	**9.50**
	4	**3.5**	**3.57**	**3.52**
No.3	**2**	**6**	**6.01**	**5.99**
	3	**8**	**8.02**	**8.01**
	4	**2**	**1.94**	**1.97**

3.7 DISCUSSION

The winter coats of the Shetland ponies ranged in length (median for different areas of the body) from 2 to 4 cm and were similar in length to those of mature Sable Island ponies, 4 cm (Welsh, 1975), but relatively short in comparison to those of Welsh/Shetland cross pony mares, 8.5 cm (Kooistra and Ginther, 1975) (Table 3.3). The summer coat lengths (median) of the Shetland ponies, 0.35 - 1.5 cm, were also relatively short compared with that of the Welsh/Shetland mares, 2.8 cm (Kooistra and Ginther, 1975) which was the only other measure available for comparison.

The site of measurement can bias the results, but Kooistra and Ginther (1975) did not report the body area where they made their measurements. The body areas where the coat was longest on the Shetland ponies were the interscapular region in the summer, and the semitendinosus region in the winter. It is unlikely that Kooistra and Ginther (1975) chose these areas as their sampling sites, as the neck and rump have been used more often when only one site has been measured (Ellis, 1975; Cymbaluk, 1990; Cymbaluk and Christison, 1993).

The maturity of an animal can influence coat length, immature animals having longer winter coats, but the Welsh/Shetland cross mares were all mature animals (Kooistra and Ginther, 1975). Environmental temperature is an important factor in the control of hair growth, therefore the colder ambient temperatures in North America (Kooistra and Ginther, 1975) may have been the underlying reason why the hair on the Welsh/Shetland ponies was longer. However, the summer temperatures were higher and the summer hair coat was also longer than that of the Shetland ponies. Breed differences in coat length and density have been shown in both horses and cattle (Cymbaluk, 1990; Gilbert and Bailey, 1991). Therefore, the differences in coat length between the Shetland and the Welsh/Shetland cross pony mares may be inherently different which would explain why these differences were also evident in the summer coat.

Young and Coote, (1973) measured the average coat depth of a mature riding horse (~ 500 kg) from 27 sites on the trunk and 6 on the legs. In early winter (month not stated) the average depth was 0.93 cm, this increased as the winter coat developed, to 1.8 cm in March. The March measurement for the riding horse, 1.8 cm, was below the the mean values of 3.07 (s.e. 0.2) and 2.64 (s.e. 0.19) cm measured from 17 sites on the trunk of the two Shetland ponies. If the environmental conditions were the same, this would be expected on the basis that the surface area to volume ratio of a larger horse (~500 kg) would result in a lower rate of heat loss in comparison to a smaller horse such as the Shetland ponies. Therefore, a larger animal would not require as thick a coat as the small ponies in order to minimise heat loss. However, the riding horse was acclimatised to the much colder, although dryer, Canadian winter, therefore it may have been expected to develop a coat which was at least as thick as that of the Shetland ponies, which were acclimatised to a relatively warm and wet U.K. winter. Breed differences may again be an important factor.

When the median values of the depth of winter coat on the Shetlands, 2.0 - 2.63 cm, were compared to that of the Welsh/Shetland mares, 2.1 cm (Kooistra and Ginther, 1975), the values were similar, but if compared to the mean values over the body of the Shetlands (2.64 - 3.07 cm) the Welsh/Shetland cross ponies had less deep coats. This may well be a result of the unreported sampling site used by Kooistra and Ginther (1975). For instance, the depth of coat over the back, lumbar and sacral regions of the two Shetland ponies were 2.75, 2.0 and 2.0 cm for pony No. 1 and 2.0, 1.5 and 2.0 cm for pony No. 3, whereas the equivalent lateral regions, i.e. the ribs (costal), flank (lateral abdominal) and femoral regions tended to have deeper coats; 3.5, 3.0 and 2.0 cm for pony No. 1, and 2.75, 2.5 and 2.5 cm for pony No. 3 (Appendix 3.2). The dorsal surfaces of small ponies are more easily accessible for measurement and, from comparison with measurements from the two Shetland ponies used in this thesis, the coat depths reported by Kooistra and Ginther (1975) may relate to the dorsal surfaces of their Welsh/Shetland cross pony mares.

The median depth of the summer coat on different areas of pony No.3 ranged from 0.2 to 0.4 cm and was generally greater than the depth of 0.2 cm reported for the Welsh/Shetland mares. Once again, this may have been due to the site at which the measurements were made.

In order that future measurements of the length and depth of hair coats may be comparable, the number and position of sampling sites should be standardised.

The observation that M&M ponies have a single-layered coat in the summer and a double-layered coat in the winter i.e. an undercoat and an overlying layer of guard hairs (Baker, 1993) may be explained on the basis of the range of fibre lengths in each coat. In the winter coat the average range of fibre lengths from the back region was from 13.2 mm (s.e. 2.77) to 58 mm (s.e. 19.0), a difference of 44.8 mm; in the summer coat the range was from 6.7 mm (s.e. 0.56) to 17.2 mm (s.e. 0.5), a difference of 9.9 mm. Therefore, the differences in length between the longest and shortest fibres increase in the winter coat in comparison to the summer coat (Plates 3.10 and 3.11). Although the majority of fibres are of a fairly uniform length, the winter coat probably functions like a double-layered coat simply due to the increased range of fibre lengths, even though horses do not have the secondary fibres associated with seasonal undercoats in other species (Blazej et al., 1989; Ryder, 1973). Distinct groups of fibres of different lengths were not evident in the carded hair samples in Plates 3.10 and 3.11, neither was there a peak in the number of fibers of fine diameter (Figures 3.6 and 3.7), both facts which do not support the presence of a true undercoat in Shetland ponies. These findings support the observation of Blazej *et al.* (1989), that the undercoat in horses is indistinguishable from the rest of the coat.

Unfortunately, measurements of both length and diameter were not available for individual fibres. This combination of parameters would identify populations of fibres which have distinct combinations of length and diameter, and help to explain in more detail how the structure of the coat is related to its various functions. The fibres of exceptionally large diameter (~200 m, Figure 3.7) are most probably tactile vibrissae (Sisson and Grossman, 1975).

It is perhaps surprising that the seasonal difference in coat depth over the back of the Shetland ponies, 5-7 fold decrease in summer, was not associated with a decrease in the number of fibres/cm^2. However, other parameters did change significantly. The length and density (mg/cm^2) of the summer coat were approximately one third those of the winter coat. These changes, in combination with the decrease in the difference between the maximum and minimum fibre lengths in the summer coat, probably account for the seasonal differences in coat structure.

The tensile strength of the individual hairs and their arrangement with respect to their lengths and diameters may be an integral part of the water-shedding capabilities of the hair coat. Because the coat is made up of hairs of varying length, the tips of the longest hairs at any one place will be the last to be drawn together by the surface tension of water as it drains down the fibres. The result will be the triangular tufts or tiles seen in Plate 3.1. The amount of water used to soak the ponies during the coat wetting experiment, equivalent to 188 mm of rain in 10 minutes, was much greater than would be expected under field conditions in the U.K.. The annual rainfall for the area of the Veterinary Field Station is 895 mm (Francis, 1981). Even so, the coat was able to shed this volume of water very easily, as became evident during the training of the animals. Hosing the ponies, without brushing, resulted in the water flowing through the outer layer of the coat. At the end of 10 minutes of hosing, the coat was dry only a couple of millimeters below the wet outer surface. Under these extreme conditions, and also under natural rainfall, the layer of sebum with which each hair fibre is coated (Scott, 1988) may also have an important role in keeping water away from the skin surface. Although the size of the sebaceous glands is known to be greater over the rump and the dorsal surface of the neck (Scott, 1988), seasonal variation in sebum production has not been fully explored or related to diet.

Individual variation in coat characteristics between different breeds of horses have been described by Cymbaluk (1990), but were also measured between individual ponies of the same breed in this study. The body regions with the longest coat fibres differed (Appendix 3.5); dorsal cervical (two ponies) compared to the costal region (three ponies), as did the length of winter coat over the lower limbs (Appendix 3.2). Also, whilst fibre diameter changed significantly between seasons for two individuals, the median values for each animal were consistently low or high in relation to the other ponies, regardless of season (Table 3.7, Figures 3.6 and 3.7). The results of an investigation of hair coats in cattle suggested that selective breeding for some hair coat characteristics may be possible (Gilbert and Bailey, 1991). Such selection may not be necessary in M&M ponies, beyond the positioning of facial and flank whorls and the requirements for coat colour, but may be useful in lighter breeds where breeding stock live outside. However, even young standardbred horses can adapt to out-wintering in sub-zero temperatures if adequate acclimatisation periods and feeding levels are given (Cymbaluk and Christison, 1989).

There appears to be an inverse relationship between cold stress and coat length, depth and density (Ellis, 1975; Pollock, 1980; Cymbaluk, 1990) and, as a cold stressed animal is likely to be vasoconstricted, one possible regulator of coat length could be skin temperature. This proposal is supported by the measured length of the hairs over the semimembranosus region of Shetland ponies No.1 and No.3 (Appendix 3.2). The semimembranosus region lay under the sides of the tail of both ponies and had a coat length of 0.25 and 0.5 times the length of the adjacent, but uncovered semitendinosus region in pony No. 1 and No. 3 respectively. Coat depth was also less, 0.2 compared to 2.5 cm in the semitendinosus region for pony No.1, and 0.2 compared to 1.5 cm in pony No.3. It is probable that the combined insulation of the thick tail plus the underlying hair coat were equivalent to that of the adjacent hair coat alone.

The importance of the combination of different layers of insulation became evident in Experiment 3.2 when measurements of insulation were made when the hair coat was wet or dry. The external thermal insulation, I_e, decreased significantly ($P<0.05$) after soaking (Table 3.10) whilst body tissue insulation, I_t, increased ($P<0.01$). The reasons for the change in coat insulation are the replacement of trapped air with water, which is a poor thermal insulator, and a decrease in coat depth (~50 %).

After soaking, when cold water was repeatedly reaching the skin surface, the temperature of the skin surface had cooled significantly by approximately 10 ^{o}C. This was most probably due to a combination of direct removal of heat by the cold water and vasoconstriction in response to this cooling. However, as the temperatures over the dry neck did not decrease significantly, the effect was probably localised to the wetted areas.

Another possibility is that the insensible heat loss of the pony increased due to the latent heat of vaporisation of water evaporating from the wet coat surface, and that this was responsible for maintaining a lower skin temperature. If no change in the cutaneous blood supply to the wet areas had occurred then a gradual increase in skin temperature could have been expected after the 10 min of soaking. However, there was no significant change in skin temperature 3 h after soaking (Table 3.8b). It appears, therefore, that vasoconstriction had occurred, even if latent heat loss from the coat surface also contributed to the decreased skin temperature.

As a result of the changes in the I_t and I_e of the wetted area, the total insulation of the wet back and rump did not differ significantly from that of either the dry neck, or the whole pony before it was wetted (Table 3.10). This seems logical, as the environment had not changed (measured by ambient temperature), neither did the metabolic rate of the ponies, only the condition of part of their body surface. Therefore, it could have been expected that the total insulation of the animal would remain the same, even if this involved localised changes in I_t and I_e.

The fact that the Shetland ponies were able to maintain their thermal equilibrium by using non-metabolic methods indicates, by definition (Webster, 1974; Ehrlemark, 1988) that they were not below their lower critical temperature, even at the lowest temperatures of this experiment, 2 ^{0}C. The use of Webster's (1974) equation for the calculation of LCT was, therefore, inappropriate as it assumes that the animal is maximally insulated i.e. maximally vasoconstricted, is losing a minimum of heat by evaporation and has not yet increased its metabolic rate above the thermoneutral level. Therefore, it is not a predictive equation, it only describes the ambient temperature (Table 3.11), and simplifies (Appendix 3.9) to give:-

$$\text{LCT} = T_a \text{ (ambient temperature)}$$

Morgan (1995) used a slightly modified version of Webster's (1974) equation, which simplifies to the same outcome, to calculate the LCT of horses acclimatised to temperatures between 15 and 20 °C. However, Morgan (1995) also measured the rates of evaporative (skin plus respiratory) and sensible heat loss from these horses at a range of air temperatures above and below the range to which they were acclimatised, and from this was able to estimate LCT as the temperature at which heat loss was minimal. Of the four horses and one pony used, the Shetland pony had the highest LCT, 20.7 °C, followed by four standardbred horses with LCT's of 19.6, 18.3, 17.3 and 15.2 °C. Therefore, the range of temperatures to which the animals were acclimatised appeared to include their LCT. It may be that in summer, the thermoneutral zone of horses is designed to make allowances for the additional heat load possible from solar radiation (300 W/m^2 in summer in western Scotland) and, therefore, LCT is close to average summer temperatures. This is one explanation of Morgan's (1995) results.

McBride et al. (1983) estimated the LCT of quarter horses by measuring their metabolic rate under controlled conditions by varying the temperature inside a climate chamber. The quarter horses were kept outdoors in a Canadian winter at ambient temperatures which ranged from an average minimum of -10.8 ^{o}C to an average maximum of -2.9 ^{o}C. Lower critical temperature was estimated to be lower than -10 ^{o}C, and close to -20 ^{o}C as this was the temperature at which metabolic rate was significantly increased. This indicated that, for the quarter horses, their LCT was not more than 10 ^{o}C below the range of ambient temperatures to which they were acclimatised.

Therefore, the quarter horses had a thermoneutral zone which extended at least from +10 ^{o}C to -10 ^{o}C, with an estimated LCT of -15 ^{o}C (McBride et al., 1983). It therefore seems unusual that the horses and pony in Morgan's (1995) study should have had LCT's within their acclimatised range. Equally it suggests that the LCT of the Shetland ponies studied in this thesis would be at least 5 ^{o}C below the average ambient temperature during the experiment, which was approximately 3 ^{o}C, giving an estimated LCT of -2 ^{o}C.

Young and Coote (1973) had made a similar study using a climate chamber and measuring metabolic rate, and estimated the LCT of a mature riding horse during a Canadian winter to be -9.4 ^{o}C, approximately 5 ^{o}C higher than the value proposed by McBride et al. (1983) who also worked at the University of Alberta. In early winter (month not given) this horse had an LCT of 0 ^{o}C and its metabolic rate increased by 10% when the horse was exposed to a temperature of -7 ^{o}C. This was in comparison to the metabolic rate measured at 21 ^{o}C. As the winter progressed, the hair coat became thicker and the animal gained weight, approximately 50 kg, which was assumed to represent subcutaneous fat (Young and Coote, 1973), and by late winter (March) when measurements were repeated, the estimated LCT had decreased to -9.4 ^{o}C. Values of I_t and I_e for this horse were only reported at temperatures below LCT, but both types of insulation increased as the winter progressed. At 14 ^{o}C below LCT in early winter I_t = 0.315 and I_e = 0.717 ^{o}C m^2 W, in late winter at 10 ^{o}C below LCT I_t = 0.421 and I_e = 0.886 ^{o}C m^2 W. These give total insulation values of 1.032 and 1.307 ^{o}C m^2 W. Although the insulation of Young and Coote's (1973) horse is not directly comparable to that of the Shetland ponies in the current study, because they were not below LCT and therefore not maximally insulated, it is interesting that the total insulation of the Canadian horse was at least double those of the Shetland ponies; 0.446 - 0.519 ^{o}C m^2 W

(Table 3.10). The difference in I_t in horses of comparable weight (~500 kg) in winter and summer can be illustrated using the value from Young and Coote's (1973) horse, 0.421 ^{o}C m^{2} W in March, which was approximately 5.5 times the average I_t for Morgan's (1995) horses which was 0.076 ^{o}C m^{2} W. This may indicate that horses are capable of a seasonal 5.5 fold decrease in I_t with a ~25 ^{o}C increase in LCT. However, studies extending over the whole year, and using the same horses under constant managment conditions are needed in order to confirm this possibility.

Although Young and Coote (1973) reported that the riding horse used in their study lived outdoors, they did not report the ambient temperatures during that winter, therefore the LCT's which they reported could not be related to the ambient temperatures to which their horse was acclimatised. This means that the only relationship between LCT and ambient temperature in mature horses is that from McBride et al.'s (1983) study, which indicates that LCT may be ~5 ^{o}C below average minimum ambient temperatures.

Until the thermoneutral zones of horses and ponies acclimatised to average seasonal temperatures in the U.K. have been established, the only information available on the energy demands of the UK environment are the general indicators of heat loss from thermal models of horses in an Aberdeenshire winter (CRB & AAPCA, 1991; MacCormack and Bruce, 1991). However, definitions of the categories of mild, average and harsh winter conditions used in the publication resulting from this study (CRB & AAPCA, 1991) would be required in order to apply the recommendations accurately.

The thermal environment, as perceived by livestock with a full winter coat, will not be the same as that perceived physically by those who care for them. Equally, wind-chill factors reported for humans (Collins, 1983) will be greater than those relating to livestock. A more appropriate index for use with out-wintering, acclimatised horses is the wind-chill index for cattle in winter coats published by Ames and Insley (1975). Whilst the effect of wind on the rate of heat loss in horses is currently unknown, the fact that cattle in ambient temperatures of 0 to 10 ^{o}C in still air showed the same metabolic response as the Shetland ponies under similar conditions in this study, i.e. no increase in metabolic rate in response to wetting (Christopherson, 1981), indicates some similarity in these species in their responses to winter weather conditions. Until a wind-chill index has been described for horses, the cattle index could be combined with the information from which the definitions of mild, average and harsh winters were derived by McCormack and Bruce (1991), to create an exposure index. This would facilitate use of the feed recommendations published from the work by McCormack and Bruce (1991) (CRB & AAPCA, 1991).

3.6 Conclusions

The thermoneutral zone and lower critical temperature of horses and ponies have not been fully described. As the LCT relates to energy requirements, and therefore food requirements, it is an important area of equine physiology, but remains poorly described except for very cold areas such as the western prairie states of Canada (Young and Coote, 1973; McBride et al., 1983). The LCT of horses and ponies in temperate regions with wet, windy winters remains undefined.

As horses are kept successfully in all climates ranging from sub-arctic to tropical, and as M&M ponies as well as thoroughbreds are exported to and from warmer climates, studying the changes in the hair coat and physiology of horses as they acclimatise would help to explain the ability of horses to adapt to the environment, and therefore to survive in many different habitats.

3.7 Future work

Standard sites of measurement for the description of the hair coats of horses and ponies need to be adopted so that the results of different studies may be compared in a meaningful way.

Studies of the hair coat and thermoregulation need to be extended in the following areas:-

1 Seasonal coat development in relation to age, energy intake, climate, reproductive status and reproductive success.

2 The influence of breed on the above, plus intra breed variation.

3 The mechanical effects of precipitation on the hair coat in relation to the biomechanical properties of the coat and its component fibres, and its water-shedding and thermal properties.

4 The water repellent properties of the sweat/sebum emulsion and the relation of the diet to the seasonal composition and quantity of sebum.

5 The influence of climatic variables; wind speed, radiation, precipitation; on the thermal properties of the coat in different seasons.

6 The influence of normal management procedures on LCT, such as the clipping and rugging of horses and ponies wintered indoors and outdoors, requires investigation.

CHAPTER 4
THE BEHAVIOUR OF FREE-LIVING HORSES

4.1 INTRODUCTION

Free-living horses live in very different environments, from the deserts of Namibia (Sneddon, 1992) to the forested foothills of the Canadian Rockies (Salter and Hudson, 1982). This suggests that their behaviour is flexible enough to enable them to harvest enough energy under a wide range of climatic and nutritional conditions. The energy expenditure of free-living horses depends on many different aspects of their environment which influence the relative amounts of time given to feeding, travelling and resting. These include both daily and seasonal changes in the climatic and nutritional environment, and in social and reproductive activities (Duncan, 1980).

The energy costs of different activities may be calculated from either their duration or the distances covered whilst moving around (Osuji, 1974). Although there is a considerable amount of information on the duration of different activities, there is very little on the distances travelled daily or on the speed of movement either whilst feeding or travelling at a steady pace. Free-living horses generally live in areas where their essential resources of food and water are in localised areas of their normal range (Pollock, 1980). Other areas are used for resting in shade, sheltering from wind and rain, avoiding insect pests and reducing heat stress (Berger, 1986; Keiper and Berger, 1982). The distances which horses travel each day vary depending on how far and how frequently they travel to these different areas. Estimations of energy expenditure resulting from this kind of activity could be made from the speed of movement and the distances travelled in specific areas and seasons.

The locations used as resting areas appear to be chosen in relation to prevailing weather conditions and offer either a means of reducing or increasing the rate of heat loss. In different seasons, the relative amounts of time occupied by feeding and resting may reflect the costs involved in feeding relative to the food energy gained, and the energy conserved by resting (Kaseda, 1983a). The aim of this thesis was to estimate the daily energy requirements of free-living Mountain and Moorland ponies in the U.K. from the amount of time they spent in feeding, travelling and resting, and the total distance moved. These aspects of their behaviour appear to be influenced by weather conditions, therefore, observations made during the behaviour study were repeated in contrasting seasons, and concurrent records of weather conditions were kept.

4.2 LITERATURE REVIEW

In the following sections all *E. caballus* will be referred to as horses, whatever their size, unless the information refers to one particular breed which is usually referred to as a pony, such as the New Forest pony.

4.2.1 24 HOUR TIME-BUDGETS

It is usual to describe the proportion of time which animals use for different activities as a time-budget (Boyd, 1988). A time-budget may be based on any period of the day or night, but when estimating daily energy requirements the 24 hour time-budget is most appropriate. However, as such reports for horses are relatively few, daylight and nocturnal observations have also been included in the following review.

Feeding is the predominant behaviour seen in horses, frequently occupying around 70 % of 24 hours, but varying seasonally from 50 to 80 % (Doreau, Martin-Rosset and Petit, 1980; Mayes and Duncan, 1986; Pratt, Putman, Ekins and Edwards, 1986).

Although horses feed mainly between first and last light (the beginning of dawn to the end of dusk) with a midday peak, night feeding forms a significant proportion of the total feeding time (Welsh, 1975; Doreau et al., 1980; Houpt, O'Connel, Houpt and Carbonaro, 1986). The peaks of activity are more pronounced in summer than in the other seasons when the amount of feeding varies less during daylight (Doreau et al., 1980; Kaseda, 1983a). Reports indicate that feeding occupies 70 % and 50 % of time during daylight and dark respectively, except for the summer months when heat and blood-sucking flies can reduce feeding in daylight to 50 % by decreasing feeding time in the early afternoon (Arnold and Dudzinsky, 1978; Keiper and Keenan, 1980; Rubenstein, 1981; Kaseda, 1983a; Mayes and Duncan, 1986).

The temporal pattern of feeding varies seasonally as the main feeding periods follow the changing times of dawn and dusk (Doreau et al., 1980; Mayes and Duncan, 1986). Welsh (1975) recorded a unique incident when, in response to an afternoon eclipse of the sun, one group of ponies moved rapidly to their habitual night time area, only to return to their original location when the sky lightened again.

When not feeding, horses are usually resting (Kaseda, 1983a, Houpt, O'Connel, Houpt and Carbonaro, 1986). Adult horses stand still for approximately 28 %, and lie down for 1.2 to 7.2 % of 24 hours (Duncan, 1980). Studies which have distinguished between standing alert and standing resting (Boy and Duncan, 1980) indicate that standing resting represents one half to two thirds of all standing behaviour (Duncan, 1980; Boyd, Carbonaro and Houpt, 1988), and that stallions spend more time alert than mares. Measurements of the energy cost of standing have not distinguished between alert and resting states, therefore, in this study, all standing behaviour was recorded under one category.

Most lying down occurs between midnight and 04:00 h, a resting period common to various types of horse in different habitats and seasons (Doreau et al. 1980; Keiper and Keenan, 1980; Houpt, O'Connel, Houpt and Carbonaro, 1986). Resting periods are usually associated with an increase in social activity, such as mutual grooming, because the animals are closer together (Tyler, 1972). Suckling occurs throughout the 24 hour period (Boyd, Carbonaro and Houpt, 1988).

Horses mostly move at a walk unless disturbed into flight by a potential threat (Baker, 1993), although some blood-sucking flies may also cause them to run (Tyler, 1972). For horses in the French Camargue, moving at any pace occupied 5 - 6 % of 24 hours in autumn/winter and 9 - 10 % in spring/summer (Duncan, 1980). Trot and gallop only represented 4 - 7 % of this movement in summer, and 2 - 2.5 % in winter, while for stallions the proportion was 10 - 13 % at all times of the year (Duncan, 1980). The sex difference is a result of the stallions' activity in keeping and procuring mares, and is not reported where breeding groups are kept in isolation (Boyd, Carbonaro and Houpt, 1988). The influence of nocturnal resting periods on the relative amounts of movement is reflected in the greater proportion (10 %) of time spent moving in daylight compared to 4.45 % at night (Welsh, 1975; Keiper and Keenan, 1980).

The basic categories of behaviour described so far, feeding, resting and moving, are collectively termed maintenance behaviour (Tyler, 1972; Boy and Duncan, 1980). Fraser (1992) included other elements of behaviour under this description, elimination of waste, stretching, and comfort behaviour such as self grooming and rolling. Although rolling may be relatively costly in terms of energy expenditure (Mayes and Duncan, 1986) it only accounted for 0.02 - 0.05 % of 24 hours for Camargue mares (Duncan, 1980). Measures of their energy costs have not been reported, but as many of these activities are of short duration and low frequency (Duncan, 1985; Boyd, Carbonaro and Houpt, 1988), they may not contribute a significant amount to the daily energy costs.

Seasonal variation in the energy requirements of free-living ponies may, therefore, be estimated from a study of the maintenance behaviour time-budgets of these animals. However, other aspects of these behaviours (distance, speed, terrain, bite rates) need to be described so that the estimates of energy requirements are relevant to the environment in which the animals live.

4.2.2 DISTANCE TRAVELLED DAILY

Distance is a useful measure when calculating energy expenditure because, except for an uncomfortably fast walk, the net energy cost of walking (the energy needed in addition to standing) is independent of walking speed (2.2.6). However, there are few estimations of the distances travelled daily by horses (Table 4.1). As different studies have used different methods for estimating distances their results are not directly comparable, but they do illustrate the range of distances which free-living horses may move in 24 hours (Table 4.1).

The availability of water, and the location of feeding areas in relation to it, are important factors in determining daily movements (Berger, 1986). Both factors are illustrated by the 40 km journeys made 5-6 days per week by desert horses travelling to a piped water supply (Van de Merwe, 1984). At the other extreme, when Primitive horses in a Forest Reserve in Poland were fed hay in the winter and ate snow for water they only moved 0.3 km. When foraging for themselves in the rest of the year they moved an average of 2 - 2.5 km in 24 hours with a maximum of 4.5 km (Kownacki, Sasimowski, Budzynski, Jezierski, Kapron, Jelen, Jarworska, Dzeidzic, Seweryn and Slomka, 1978). These estimations did not include the distances moved whilst grazing. The daily distances reported for horses living on grassland (3 - 7 km) included both feeding and travelling between grazing, resting and watering places (Klimov, 1988; Table 4.1) and agree with the values of 3 to 10 km/day given for grazing horses (Fraser, 1992). However, Fraser (1992) did not describe his method of measurement, or specify whether his values were for pastured, domestic horses or for free-living horses.

Table 4.1; Estimated distances (km) travelled by horses during different periods of time.

Distance (km)	*Time*	*Horse type*	*Location*	*Source*
40	24 hours	Feral, Namib	Namibian Desert (SW Africa)	Van de Merwe (1984)
3 - 7	24 hours	Przewalski	Steppe reserve	Klimov (1988)
average 2 - 2.5 (range 0.3 - 4.5)	24 hours	Polish primitive	Forest reserve	Kownacki et al. (1978)
1.12 summer 1.23 winter	dawn - dusk	Feral, U.S.A	Granite Range, Nevada	Berger (1986)
0.4 summer 0.41 winter	dusk - dawn			

Berger (1986) estimated the minimum distances that groups of feral horses moved during daylight and dark from linear measurements between their positions at dawn and dusk (Table 4.1). These combined to give daily distances of 1.52 km in summer and 1.64 km in winter, the differences were mainly due to increased travel in daylight in the winter (Berger, 1986). Spring and autumn movements were very similar to those in the summer.

The only data available on the movements of free-living horses in the U.K. are those reported for New Forest ponies by Pollock (1980). The data were presented as the number of new 100 m quadrats which ponies entered in one hour, whatever the ponies' behaviour. Seasonal variation was not significant, and the mean rate of movement ranged from 1.04 new quadrats/h in winter to 1.16 new quadrats/h in spring (Pollock, 1980). Unfortunately the method of calculating distance from the movements plotted was unclear, but if movement from one quadrat to another can be assumed to equal 100 m, then these rates of movement may be equivalent to 0.029 - 0.032 m/s. The minimum and maximum rates of travel were 0.6 and 3.6 new quadrats/h (Pollock, 1980), which, using the same assumption, may equate to travelling speeds of 0.017 and 0.1 m/s. This would give a possible range for the daily distance travelled of 1.47 to 8.64 km with an average of 2.64 km. These distances are similar to the 3-7 km/day estimated by Klimov (1988) from the movements of Przewalski horses, and the average distances travelled by Primitive Polish horses in a Forest Reserve (Table 4.1).

The energy costs of locomotion are not only related to the speed and distance travelled, but also to the type of terrain (Dijkman and Lawrence, 1997). Horses may minimise the energy costs of locomotion as they usually travel between different areas by using animal tracks (Pellegrini, 1971; Pollock, 1980), and avoid rocky, boggy and very steep surfaces, even following tracks when crossing grassland (Klimov, 1988). Pollock (1980) likened the pattern of animal paths between favoured grazing areas in aerial views of the New Forest to that seen between water holes on the African plains.

The energy costs associated with the distances travelled daily by free-living horses depend, therefore, on the distribution of water and on the physical terrain. The use of paths may reduce these costs. Horses also graze their way between areas, which will add to the total daily distance moved, and may increase their frequency of drinking, and therefore the distance they travel, when hot weather or lactation increase their requirements.

4.2.3 INGESTIVE BEHAVIOUR

4.2.3.1 Drinking

While horses prefer to drink fresh water they will eat snow, drink from muddy or brackish water holes, and have occasionally been seen to drink salt water (Pellegrini, 1971; Feist and McCullough, 1976; Rubenstein, 1981; Coleman, 1982; Ralston, 1986). In summer, horses stay closer to permanent water sources, because of their increased need for water due to higher temperatures and lactation, and the seasonal lack of surface water (Pellegrini, 1971; Miller, 1980). Miller (1980) recorded how the average distance of horses from water decreased from 6.75 km at an average weekly temperature of -10 ^{o}C, to 2.75 km when the average temperature was 20 ^{o}C.

The time of day and frequency of drinking vary greatly depending on the availability of water, its distance from feeding areas, summer temperature and disturbance. Pellegrini (1971) observed that feral horses in western Nevada drank once every 48 h, and always at night due to human disturbance around the watering area in daylight. Each animal drank for approximately five minutes and, by pawing at the water, was thought to help keep the muddy water hole from filling in. While Feist and McCullough (1976) observed some groups of horses drinking at night they usually drank during daylight, although not at any fixed time. Lactating Welsh pony mares drank every 1.8 hours in hot summer weather (30 - 35 ^{o}C; Crowell-Davis et al., 1985). Under similar conditions feral horses increased their time at the water hole from a few minutes to a couple of hours (Feist and McCullough, 1976).

Lactating mares are not only providing their foals with food, but are also drinking for them as foals drink water infrequently until weaning (Crowell-Davis, Houpt and Carnevale, 1985). This probably explains why nursing mares are usually the first of a feral group to reach water (Welsh, 1975; Feist and McCullough, 1976). Horses have not been reported to permanently exclude others from water holes. Unless they were desperate for water, different groups waited their turn at a distance which did not lead to confrontation (Pellegrini, 1971; Rubenstein, 1981).

In hot weather, free-living horses may limit the distances involved in travelling to water by staying closer to watering places or by increasing the length of time they spend there. In areas, such as the New forest, where water is easily accessible throughout the year, there did not appear to be any seasonal variation in daily distance travelled (Pollock, 1980), although this aspect of behaviour has not been studied *per se*.

4.2.3.2 Grazing

The energy costs of eating have been shown to vary, in stabled horses and ponies, with the type of fodder e.g. straw required more energy per kg than hay, which required more than loose grain (Vermorel and Mormede, 1991; Vernet, Vermorel and Martin-Rosset, 1995). Also, the energy costs of intense grazing as measured in cattle, represented 20 % of the daily energy requirements of these animals compared to 6 % for moderate grazing intensities (di Marco, Aello and Mendez, 1996). Therefore, the type of food eaten and the bite rate of a horse may indicate the energy costs of eating.

Within the U.K. the reported eating habits of free-living horses were consistent both in the species of plants eaten and in the seasonal variation in plant community use. Horses are preferential grazers (Pratt, Putman, Ekins and Edwards, 1986) and the favoured grass species in the U.K. are Bent (*Agrostis spp.*), Fescue (*Festuca spp.*) and Purple moor grass (*Molinia spp.*), (Pollock, 1980; Gates, 1980; Putman, 1986; Albiston, 1987; Gordon, 1989a). Preferred grazing areas in the New Forest were close cropped to less than 20 mm (Putman, 1986) due to high grazing pressure (McDonald et al., 1995). Similar areas are created in fields grazed by horses and, from their short (10-20 mm) and even appearance, are called lawns (Odberg and Francis-Smith, 1976). Faeces tend to be dropped in the longer (100-300 mm), rank areas of grass fields, known descriptively as roughs (Odberg, and Francis-Smith, 1976). Although ponies in the New Forest do defecate outside their preferred areas of stream-side meadows, the distinction between lawns and roughs is not as clear because, in summer, cattle keep the grass in the roughs down to 50 mm (Putman, 1986). However, the ponies also grazed these areas when plant productivity was low at the beginning and end of the year, reducing the grass height of the entire area to below 20 mm (Putman, 1986).

In winter, ponies on the Island of Rhum preferred grass communities which had a greater amount of foliage, even though most of it was dead, rather than the small areas of grasses on poorer soils which had a greater proportion of live plant material (Gordon, 1989b). Gordon (1989b) considered that this choice was probably linked to their requirement for bulk as hind-gut fermentors with a relatively high passage rate compared to ruminants.

Food intake rate is related to bite size and rate (Illius and Gordon, 1990) and, as sward biomass per unit area increases, bite rate decreases (Putman, 1986). These parameters have been used to describe the grazing behaviour of both free-living and domestic horses on various types of sward (Table 4.2).

Purple moor grass (*Molinia*) grows in clumps, in contrast to the mixture of species which occur within a short sward, so feeding behaviour can be recorded specifically for this species. *Molinia* becomes unpalatable as it dies back in the autumn, and this is reflected in a decrease in bite rate from 44 to 23 bites/min (Table 4.2) as the seasons progress (Putman, 1986).

Table 4.2; Bite rate (bites/min) of horses feeding on grass swards of different lengths, and on some browsed plants.

Grass length (mm)	*Bite rate (bites/min)*	*Sward/plant type*	*Source*
<20	43 - 72	New Forest grasslands	Putman (1986)
30	47 - 54	seeded pasture	Myers (1994)
<50	44.9	seeded pasture	McCracken (1992)
50 - 100	39.5	seeded pasture	McCracken (1992)
>100	24 - 28	seeded pasture	McCracken (1992) Myers (1994)
Browse	23 - 44 13 - 22 5 - 8	*Molinia* *Calluna spp.* (heather) *Ulex spp.* (gorse)	Putman (1986)

4.2.3.3 Browsing

In the U.K. ponies have been observed to eat many kinds of plants other than grasses (Pollock, 1980, Putman, 1986; Gordon, 1989a; Gill, 1991). These sources of food tended to be used when grasses were no longer productive in winter and early spring, or, in the case of droughts, at the end of summer when grasses still growing in marshy ground were eaten (Collery, 1974; Pollock, 1980; Gordon, 1989a; Gill, 1991). The seasonal pattern of plant use varies and may be related to plant productivity and available nitrogen (Putman, 1986). Sap begins to rise in some trees and shrubs before grass regrowth in e.g. streamside lawns (Pollock, 1980), which may explain the use of broad leaved trees in spring, but perhaps not the use of gorse in autumn.

Gordon (1989a) argued that it would not be energetically efficient for horses to eat plants with a higher lignin content as they require much more mastication before they can be swallowed. However, fibrous and woody plants were frequently reported to form part of the diet of free-living horses. Such plants may be included because, although horses may have a limited ability to be selective whilst grazing (Gordon, 1986), their prehensile upper lip makes them capable browsers. They can therefore select the leaves and growing tips from shrubs, trees and bracken, or find nuts in leaf litter, all of which are the most nutritious and least woody parts of the plant. Bite rates of ponies browsing heather (*Calluna*), and gorse (*Ulex* spp.) were much lower than when they were grazing (Table 4.2). This is probably a result of the increased time taken to both select and chew the food.

Browsed species have included heather (*Calluna* spp.), shrubs such as gorse (*Ulex spp.*), broom (*Cystisus scoparius*) and blackberry (*Rubus ulmifolius*), and trees such as holly (*Ilex aquifolium*), hawthorn (*Crataegus monogyna*), and, to a lesser extent, willow *(Sallix spp.*) (Pollock, 1980; Albiston, 1987, Gill, 1991; Baker, 1993). Holly was browsed during winter in the New Forest and broad leaves were taken in spring and the end of summer (Putman, 1986). Leaf-litter and bark have also been included in the diet (Kaseda, 1983a; Fraser, 1992).

Rushes (*Juncus* spp.) and bracken (*Pteridium aquilinum*), which contains a cumulative poison (thiaminase; McCarthy, 1987), were commonly a significant part of the diet in different seasons (Collery, 1974; Albiston, 1987; Baker, 1993). Mosses were reported to be important to New Forest ponies, and along with bracken, formed up to 25% of the diet at the end of summer (Gill, 1991). Highland ponies on the Scottish island of Rhum increased the proportion of their feeding time spent eating seaweed to 6.4 % in the winter in comparison to 1.1 % in the autumn (Gordon, 1989a). Fraser (1992) suggested that the reason why horses ate seaweed was to gain salt. However, as salt requirements are usually highest in the summer because of its loss in sweat, and these ponies were not seen to eat seaweed in spring or summer there must have been an alternative, or at least an additional reason for their eating it.

The only roots which horses in the U.K. have been recorded to eat were those of thistles (Fraser, 1992), although Collery (1974) observed Connemara ponies digging up and eating some unidentified roots in boggy ground. In the U.S.A. Feist and McCullough (1976) observed horses digging up and eating the roots of Winter fat (*Erotia lanata*), the upper parts of which were also highly palatable, and milk vetch

(*Astragalus kentrophyta* and *A. Gilviflorus*), also known as locoweed which, like bracken, has a cumulative poison (McCarthy, 1987).

Coprophagy is a normal component of the behaviour of young foals, which are thought to enrich their population of gut microbes from their dam's faeces, but is not considered normal for adult equids except as a sign of low protein intake or starvation (Francis-Smith and Wood-Gush, 1977; Lewis, 1995). Both factors may have been involved when adult and yearling feral horses ate old, dry faeces in winter (Feist and McCullough, 1976). Faeces are relatively nutritious and contain 40-60% total digestible nutrients (Ralston, 1986). A free-ranging adult Highland pony has been seen to consume a freshly voided pile of faeces in summer when he was in good condition and food was in abundant supply (Booth, 1994), but this behaviour has not been reported for other free-living adult horses in the U.K..

4.2.3.4 Eating soil

Although infrequent, and therefore probably of minor importance in relation to energy expenditure, soil-eating appears to be a normal component of the behaviour of horses and is, therefore, reviewed here.

Horses generally avoid eating soil when grazing (Ralston, 1986), perhaps because of the discomfort of grinding grit between their teeth. Feral horses tend to show accelerated tooth wear in comparison to stabled horses because of the greater amount of grit and siliceous plant material in their diets (Feist and MCullough, 1976; Welsh, 1975; Berger, 1986). Sand colic is another consequence of ingesting sandy soil whilst feeding or drinking (Raoofi, Nadalian, Sharifi, 1996). It is commonly proposed that horses seen eating soil are lacking some component of their diet, perhaps mineral salts or trace-elements. However, a deficit of sodium chloride is the only one which horses have been able to correct under experimental conditions (Ralston, 1986).

Soil eating is most commonly reported in the summer and horses seen eating sea foam on a beach were thought to have a need of salt (Welsh, 1975). The same animals also ate exposed patches of heavy organic soils. Lactating, Welsh pony mares ate clay and humus on summer pasture (Crowell-Davis et al. 1985), and a feral stallion was seen once to eat the clay at the bottom of a drying water hole (Feist and McCullough, 1976).

4.2.4 ENVIRONMENTAL INFLUENCES ON BEHAVIOUR

4.2.4.1 Weather

The effects of wind and rain were greater when they occurred together, resulting in a decrease in the time spent feeding and in horses turning their hindquarters into the wind (Arnold and Dudzinsky, 1978; Fraser, 1992). The response of *E. Przewalski* was different to that of *E. caballus* in that they moved into the wind and rain and increased grazing activity (Klimov, 1988). Klimov (1988) suggested that this may be a method of increasing water intake in a desert animal, central Asia being a relatively dry region. Ponies on Sable Island, off the coast of Nova Scotia, were seen to graze, whilst covered in snow, in winds up to 68 kph, with more than half of the animals facing into the wind (Welsh, 1975). However, once wind speeds were between 96 - 112 kph all ponies were grazing with their hindquarters towards the wind-driven snow (Welsh, 1975). After snowfall horses generally feed in areas exposed to the wind as the snow cover is, at least partially, blown off the vegetation (Pellegrini, 1971; Welsh, 1975; Berger, 1986). Duncan (1983) noted that horses were particularly sensitive around their faces and thought that this may have been why, in cool weather, they grazed with their hindquarters into the wind.

When horses were resting they preferred windy areas in hot weather but protected areas in winter (Pratt et al., 1986; Kaseda, 1983a; Berger, 1986; Duncan, 1983). Shrubs, hedges, woodland and topographical features such as sand dunes have all been used as shelter from the wind in colder seasons (Welsh, 1975; Kaseda, 1983a; Albiston, 1987; Baker, 1993). Welsh (1975) reported a higher survival rate of foals in larger groups and proposed that this may be partly due to the greater degree of physical shelter gained within a larger group during winter and spring. A later report suggested that horses seen standing together in large groups in winter on the Asian steppes may also be benefiting from the shelter of each other (Langlois, 1994). Even in a moderate climate, cooler weather and rain altered resting behaviour; in Camargue mares the proportion of lying decreased and standing increased (Duncan, 1985). Pony mares in spring and summer in the U.S.A. were observed to increase the time they spent lying after a period of cold and/or wet weather (Crowell-Davis, 1994). As horses appear to have a basic requirement for paradoxical sleep, which only occurs when they are lying flat, this may be a compensatory increase for sleep lost during wet weather (Belling, 1990) when they appear reluctant to lie on wet ground.

Although the time spent resting in shelter (Duncan, 1985), and the benefit which shelter gave in terms of reduced wind speed and therefore reduced wind chill (Berger, 1986) have both been suggested as means of saving energy, there do not appear to be any studies in which the actual reduction in wind speed at preferred sites has been measured at the time the animals were there. This would be important in estimating the energy saved by reducing exposure in this way.

4.2.4.2 Blood-sucking Flies

Throughout the warmer months many diptera in which the females require a blood meal from mammals will include horses in the species on which they feed. Horse and Deer flies (*Tabanids*), midges (*Culicoides*) and black flies (*Sulidae*) are common pests of horses in the U.K. whilst other diptera such as keds (*Hippobosca equina*) are a problem in the New Forest (Tyler, 1972; Gill, 1994).

The activity of *Tabanids*, but not *Culicoides,* has generally been reported to result in active avoidance by horses (Tyler, 1972; Mayes and Duncan, 1986). The associated reduction in daylight feeding time represents a loss of food energy, but at this time of year ponies in the U.K. are usually improving in body condition (Pollock, 1980; Gill, 1991).

Various strategies are employed by horses to reduce the incidence of attack and to remove flies from their body, apart from self grooming (Klingel, 1972). Klimov (1988) described two general orientations seen in groups of semi-wild Przewalski horses when biting flies were active. Standing line-abreast head-to-tail, and standing in a bunch with random orientation between neighbouring animals were both thought to reduce the incidence of fly attack on individuals, but also enabled the herd to keep watch in all directions (Klimov, 1988). Mayes and Duncan (1986) describe states of increasing agitation in horses on the Camargue as the number of *Tabanids* increased, ranging from more frequent use of the tail to running around the outside of the group barging against other group members, probably in an attempt to brush off the flies. A similar behaviour described as circling was recorded in Assateague ponies, but this behaviour differed in that the ponies stood with their heads towards the centre of the circle (Ford and Keiper, 1979).

If possible, horses move away from fly habitats, such as meadows and damp areas, for the parts of the day when tabanids are most active (Duncan and Cowtan, 1980). This tends to be in early afternoon on warm (>15 ^{o}C), sunny days with low wind (Helle and Aspi, 1984). The areas chosen may or may not have shade, but are usually bare of vegetation and on high ground, where wind speed is likely to be greatest (Tyler, 1972; Keiper and Berger, 1982). Snow patches and the sea have also been recorded as insect refuges, but may also be correlated with the fact that good flying weather for *Tabanids* is also hot and still, and therefore horses may also be seeking to reduce their heat load by moving into cooler areas (Keiper and Berger, 1982). Primitive horses in Poland can spend up to five hours standing still in a lake or feeding on water-plants at its edge, but the presence of biting insects was not recorded by the authors (Kownacki et al., 1978). Duncan (1985) noted that, in warm weather horses grazed into the wind which may have helped to keep biting flies away from their faces. Moving horses also seemed to have fewer mosquitos on them, and there may have been a causal link with the increase in time spent moving in the summer (Duncan, 1985).

At peak times of insect attack, horses sometimes stand close together in very large groups, which may include several stallions and their mares (Tyler, 1972; Duncan and Vigne, 1979). While large numbers must reduce the rate of attack on individuals, *Tabanids* are strongly attracted to CO_2, which must send out a strong signal from a large group. An alternative theory originated from observations of large groups of reindeer in Norway, and suggests that the accumulated effect of the evaporating sweat, "sweat steam", from all the animals may help to repel the insects (Helle and Aspi, 1984).

Prevailing weather conditions, and attacks by blood-sucking flies may both significantly change the feeding and resting patterns of horses. Their effects on energy gain (food intake) and energy costs (thermoregulation, movement to shelter and insect refuges) should, therefore, be taken into account when the daily energy requirements of horses are estimated.

4.2.5 Aims of this study

The energy requirements of free-living horses relate to their physiological maintenance energy requirements and to the level and type of activity required to fulfill those requirements. As the maintenance behaviour of free-living horses, estimated as time-budgets, changes in different seasons, measurement of the duration and intensity of each major component of maintenance behaviour (bite rate, speed of locomotion, distance travelled) could be used as a basis for estimating daily energy requirements.

Therefore, the aim of this study was to record the time-budgets of free-living M&M ponies under contrasting environmental conditions in winter and summer in order to estimate the relative importance of different activities, and their possible relationships, in terms of energy costs and conservation. These aims included measurement of the speed of movement of walking and grazing animals and estimations of the distances they covered in 24 hrs. Other important aims included the estimation of grazing intensity from measures of bite rate and grass height, and descriptions of the micro-climate of the animals from local recordings of wind speed and temperature.

4.3 MATERIALS AND METHODS

4.3.1 INTRODUCTION

The aim of this study was to estimate the seasonal energy expenditure of free-living horses from 24 hour time-budgets of their active and inactive behaviour. The design of the behavioural study was based on two periods of observation of six Exmoor pony mares under contrasting environmental conditions; late winter (March 22nd to April 5th) and summer (July 11th to 22nd). The 24 hour time-budget was estimated from scan samples taken every 15 min which resulted in:- 4 observations x 24 hours x 3 replicates x 6 ponies = 1728 observations per season.

Concurrent records of the prevailing weather conditions were kept as a basis for estimating the role of thermoregulation in the behaviour of the ponies. More detailed aspects of feeding and movement were recorded from continuous observations of individual animals in order to estimate specific components of these behaviours, such as speed of movement and bite rate, which may affect the energy costs of these activities.

4.3.2 MATERIALS

4.3.2.1 ANIMALS AND THEIR MANAGEMENT

The study group consisted of six Exmoor pony mares, registered with the Exmoor Pony Society, which were pregnant in the winter and lactating in the summer (Table 4.3). Management procedures, such as worming and foot-trimming, were carried out when animals were gathered to the farm for allocation to stallions or for the inspection and branding of the foals. Foals were removed from the herd at the end of autumn. A stallion and one barren mare ran with the six mares under observation, but behavioural data from these animals were not included in this study.

These animals ranged over approximately 17 hectares of rough grazing (latitude 54° 55', longitude 2° 37'; 225 - 280 m above sea level) which was fenced off in 1939 from the original hill enclosure which predated 1820 (pers. com. P. Dean). Between 1950 and 1960 the field had been limed in alternate years but, other than this, no applications of seed or fertilizer had been made. This area had been grazed by Exmoor ponies since 1957 with one break, in the summer of 1992, when it was sprayed for ragwort (*Senecio* spp.; pers. com. P. Dean). A post and wire fence formed the northern boundary (Figure 4.1), the garden of the cottage (Tortie) was enclosed by a 1.5 m high split-hazel fence, and a dry stone wall (~ 1.5 to 2 m high) extended round the rest of the enclosure. There were no trees or shrubs in the field and the few deciduous trees just inside the garden fence gave neither shade nor shelter. Locations of the various topographical features are marked on Figure 4.1, including seasonal areas of standing water (dew ponds). To the east of the quarry and Drybank Hole the sward was dominated by rushes (*Juncus spp.*).

Table 4.3; Details of the Exmoor mares in the study group.

*Name**	*Age (years)*	*Foaling date*
Beauty	**14**	**6th May**
Brandy	**9**	**6th May**
Browny	**6**	**30th June**
Friendly	**6**	**30th May**
Trim	**3**	**28th April**
Tufty	**3**	**24th April**

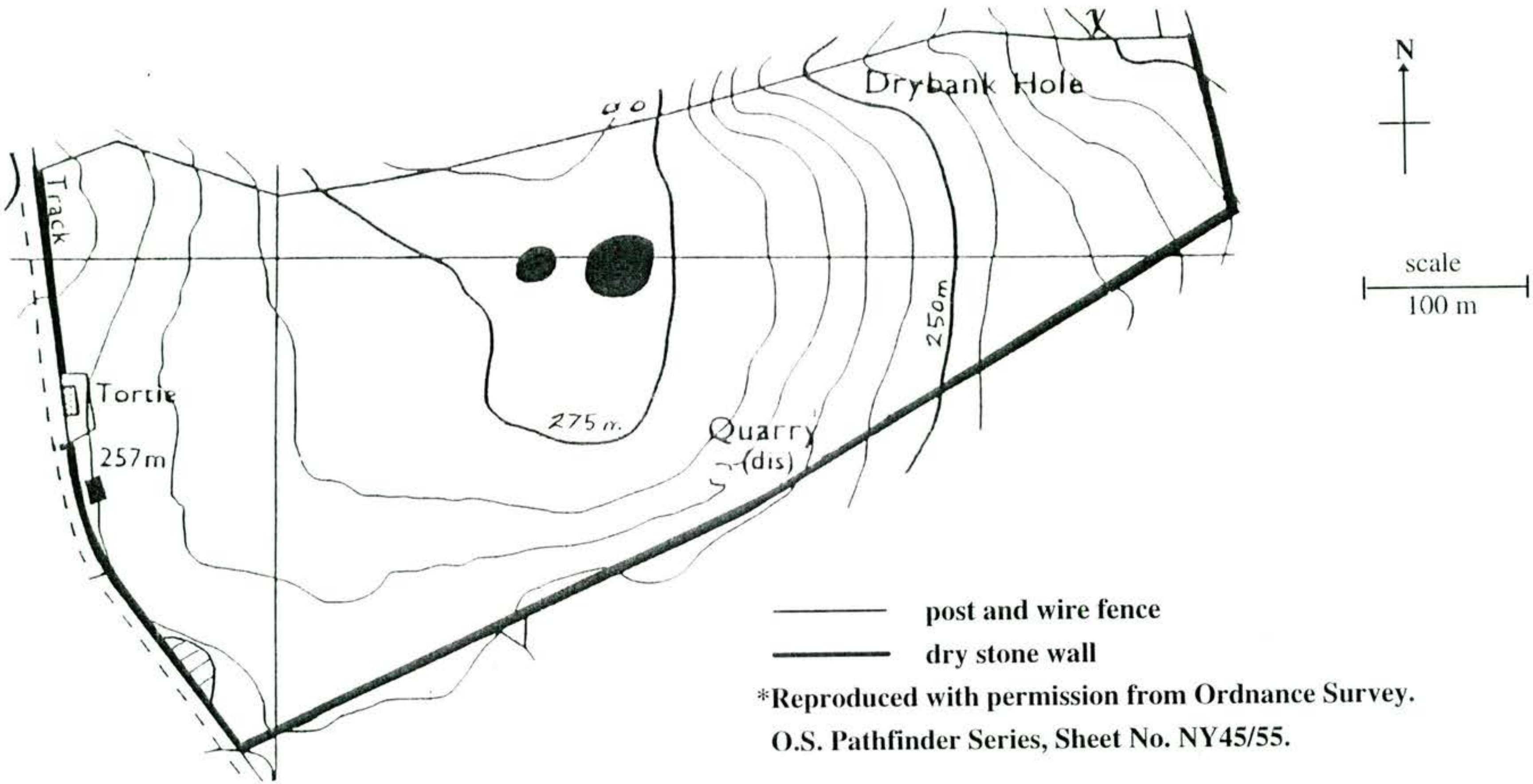
* names used as an aid to identification, not the registered names.

4.3.2.2 OBSERVERS

The author was the only observer in the winter, but in the summer she was accompanied and assisted by Catherine Brown, an Honours Zoology student from the University of Aberdeen (Brown, 1995).

Figure 4.1; Plan* of the study area.

■ water trough ● standing water (winter only) ▨ water (winter), mud (summer).



— post and wire fence

━ dry stone wall

*Reproduced with permission from Ordnance Survey.
O.S. Pathfinder Series, Sheet No. NY45/55.

4.3.2.3 FIELD EQUIPMENT

The following equipment was always carried:-

Dictaphone; Pearlcorder S925, Olympus Optical Co., Ltd. China. This was covered in a wind-sock made from felt, and a plastic bag.

Map of the field with quadrats marked (clear plastic case with shoulder strap).

Stopwatch (waterproof) with shoulder strap.

Compass with shoulder strap.

Torch; waterproof with shoulder strap (carried from sunset to sunrise).

Anemometer; hand-held, battery powered, cup anemometer.

Camera; Ricoh FF-10 zoom; automatic focus and exposure.

Additional equipment:-

Dry and wet bulb thermometer - positioned at the entrance to the field at the start of each observation period (4.3.3.6).

Sward stick (Bircham, 1981) - used to measure grass height.

4.3.3 METHODS

4.3.3.1 PONY IDENTIFICATION

Whilst Exmoor ponies are fairly uniform in colour and have no white markings at all, there were sufficient differences in size, conformation, physical appearance of the coat and pattern of the mealy patches around the eyes and muzzle to allow identification of all individuals by day or night (torchlight).

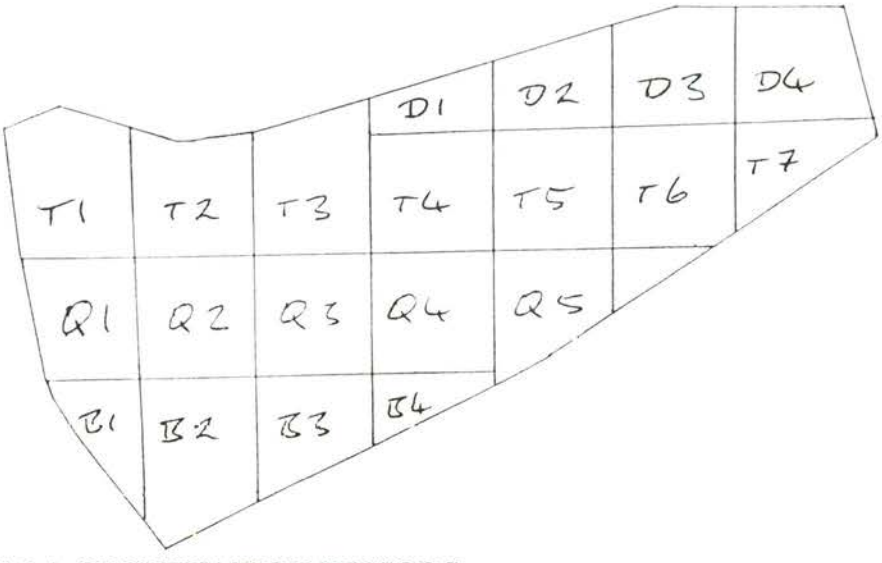
4.3.3.2 HABITUATION TO THE OBSERVER/S

The animals were frequently visited by the owners and, as they were neither fed nor handled by the observers, quickly accepted their presence. Individual animals varied in their flight distance. Observers took this into consideration in their own movements around the ponies and did not approach them directly. Most of the ponies took no notice of the torch light. Those that did were initially curious, but became disinterested quickly.

4.3.3.3 QUADRAT MARKING

The field was divided into quadrats approximately 100 m by 100 m (Figure 4.2). Distances were paced out along compass bearings, starting from the entrance to the field. Points where the boundaries crossed fence lines were marked initially with strips of white plastic tied to the fences/walls. The positions of topographical features such as animal paths, old walls and fence lines, large rocks, drainage ditches and changes in vegetation (reeds, roughs and lawns) plus surface water enabled the observer to visualise quadrat boundaries accurately. These features were equally useful in daylight or at night. The area of each quadrat, and its gradient were estimated arithmetically from the scale map (Appendix 4.1).

<u>Figure 4.2</u>; The names and locations of quadrats in the study area.



4.3.3.4 OBSERVATION PERIODS

The total observation time, of 72 hours in each season, was covered in three replicated 24 hour periods. Each 24 hour period was made up of 12 recording periods (2 h) spread over at least 4 calendar dates and are therefore referred to as composite days (Appendix 4.2). In this way the total behaviour record was more likely to be representative of the season rather than being biased towards short term climatic conditions.

In a preliminary study two hours was decided upon as the optimum observation period when using a dictaphone for recording observations, allowing for continuous use of battery powered equipment and the observer keeping warm enough in the winter if animals were mostly standing still. Observations were grouped into sessions of 10 hours, broken down into:- two hours in the field; two reorganising equipment, resting, eating etc.; two in the field; two resting etc.; two in the field (Appendix 4.2). A longer continuous break then followed for transcribing data, sleeping etc..

4.3.3.5 BEHAVIOUR RECORDING

Under the restrictions of time and number of observers, the most appropriate method for estimating the time-budget for the major components of the daily behaviour of the ponies was instantaneous scan sampling (Martin and Bateson, 1986) as this made it possible for one observer to record the behaviour of all six ponies. An interval of 15 min was used. More detailed observations were made between scan samples by watching one animal (focal animal sample) and e.g. recording its grazing or locomotory behaviour in relation to elapsed time.

24 hour time-budget

Instantaneous scan samples of the behaviour of all six ponies were made every 15 min starting on the hour. Therefore, the total number of observations in each season was 1728. The observations recorded for each animal described their behaviour as being in one of seven mutually exclusive categories (Table 4.4). The orientation of each animal in relation to the direction of the wind (Figure 4.3), and its location (quadrat; Figure 4.2) were then also recorded.

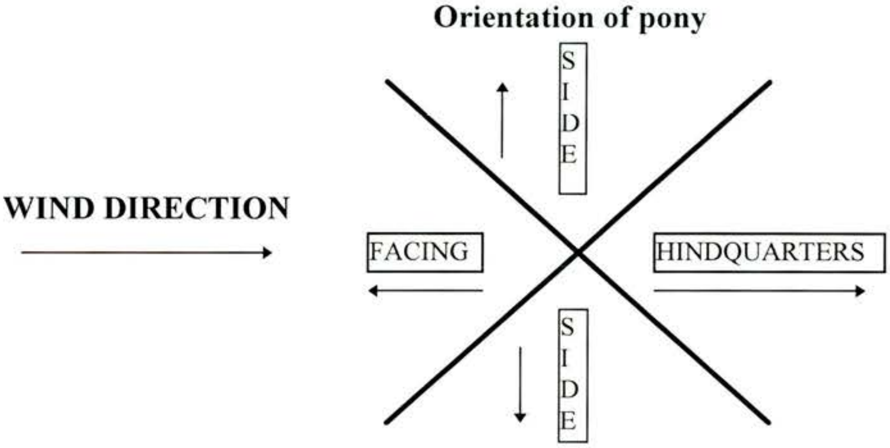
The 24 hour time-budget in both seasons was described as the relative porportion of time spent in each behaviour over 24 hours (all observations summed over all ponies / 1728).

Table 4.4; The mutually exclusive categories of behaviour recorded during instantaneous scan samples.

Category	*Description of behaviour**
Ingestion	**grazing / eating anything, and drinking**
Moving	**walking, trotting and cantering/galloping**
Standing still	**standing still; either alert or resting**
Lying down	**lying on either the sternum or the side**
Interacting	**mutual grooming**
Other	**any other behaviour observed, including suckling foals**
Missing	**animals out of sight or scan sample missed for other reasons**

*Based on Duncan (1983)

Figure 4.3; **Orientation of ponies to the wind classified according to 90° arcs.**



Temporal patterns of behaviour

To examine the occurrence of each behaviour category in relation to the daily cycle of daylight and dark, the data was arranged on an hourly basis. For each season the total number of observations in each behaviour category, except *missing*, was calculated for every hour (sum of all ponies and all composite days (Appendix 4.3). These were converted to proportions by dividing them by the total number of observations in all behaviour categories in each hour.

Behaviour recorded using focal animal samples

Grazing behaviour

Bite/step rates:-

A grazing animal was selected at random and the duration of the observation was timed using the stop watch. The start of the grazing observation was defined as the point when the animal placed one or other fore foot on the ground when taking a step. Thereafter the number of biting actions (tearing off selected herbage with teeth) were counted between each subsequent step with either front leg. The session was terminated when the pony either walked (defined as more than 2 steps forwards with the muzzle lifted above the height of the pony's knees), or performed one of the other mutually exclusive categories of behaviour (Table 4.4).

Speed of travel

grazing, walking, trotting and cantering/galloping

A stop watch was used to time (s) the grazing/walking periods for which the starting and stopping positions of a specific forelimb could be accurately located (either by obvious herbage or hoof prints). The distance was then estimated by pacing it out.

The mean length of a pace was estimated for both observers by measuring the distance covered in 10 paces and repeating this 10 times. The mean (s.e.) pace lengths for each observer were:- Booth = 0.908 (0.015) m; Brown = 0.962 (0.017) m. The appropriate correction factor was then used to calculate the distance moved by the animals, and then the speed (m/s) was calculated from the distance (m) and time (s).

4.3.3.6 THE DISTANCE TRAVELLED DAILY

The distance moved between quadrat positions

For the purpose of calculating distance, animals were assumed to be at the centre of the quadrat, therefore when moving north, south, east or west to an adjacent quadrat the distance would be 100 m. For all other moves the distance was calculated by using Pythagoras' Theorem. For each pony the total distance travelled in each of the three 24 hour periods was estimated as the sum of the distances moved in each 2 hour period. For winter and summer the distance travelled in 24 hours was calculated as the mean of the 18 estimations (6 ponies x 3 days).

Estimation of distance from the speed and duration of activities

The assumption was made that the occurrence of each behaviour as a proportion of all behavioural observations (the sum total of all scan samples for all ponies over 3 x

24 hours) would be equivalent to the same proportion of 24 hours and could therefore be expressed as time. The mean speed (m/s) at which ponies moved whilst grazing (*ingestion*) and *moving* (walk and trot) was multiplied by the amount of time spent in these activities in winter and summer to estimate the total distances travelled.

4.3.3.7 WEATHER RECORDS

Recordings of each of the following parameters were made for each two hour observation period.

Ambient temperature

A wet and dry bulb thermometer was left in shade about 15 cm above ground at the entrance to the field and was read at the end of the two hour period.

Wind speed

A hand-held, battery operated, cup anemometer with liquid crystal display was held up-wind of the observer at arms length and at head height. After activation, the anemometer recorded data for 30 s then displayed the maximum and average wind speed in m/s. Measurements were made in the most exposed area of the field i.e. quadrats Q2-Q4...T2-T4.

Additionally, if animals were in areas of reduced wind speed, measurements were taken not more than 5 m from the pony at the height of the pony's back (animals may be standing or lying), and also above the wall or out of the topographical shelter (e.g. quadrat T4 in comparison to Drybank Hole; Figure 4.1).

Climatic conditions

The following conditions were recorded at the start of each two hour observation period and then updated every 15 min if and when they changed:-

Cloud cover; recorded as the number of eighths of the sky (oktas) which would be completely covered by the total amount of cloud present (Dunlop, 1996). These figures were then converted to percentages.

Precipitation; mist, fog, drizzle, rain, hail or snow.

Sunshine;

Biting flies; *Culicoides* (biting midges) or *Tabanids* (horse-flies; Chinery, 1976).

The last three parameters were noted as present or absent and were not measured in any way.

Daylength

Sunrise and sunset were at 06:00 h and 18:00 h in the winter, and at 05:00 h and 21:00 h in the summer. Daylight was defined as the period between first and last light; 05:00 to 19:30 in winter; 03:30 to 22:30 in summer. Dawn extended from first light to one hour later, and dusk began one hour before last light (Mayes and Duncan, 1986).

4.3.3.8 SWARD HEIGHT

A sward stick (Bircham, 1981) was used to measure herbage height. Twenty measurements were made at random in as many quadrats as possible in the winter before it snowed. Up to 40 measurements were made in each quadrat in the summer. Also, 40 measurements were taken at random within each of three distinct areas of herbage identified in the summer; short grass (lawns), average grass, and long grass (roughs).

4.3.3.9 STATISTICAL ANALYSIS

Categorical data (instantaneous scan samples) were analysed using appropriate non-parametric tests; Wilcoxon signed rank, Kruskall-Wallis, Friedman two-way analysis of variance by ranks and Chi-square (Siegel and Castellan, 1988).

Normally distributed sets of continuous data (measurements) were analysed using anaysis of variance and paired t-tests. Where possible, data sets were normalised by $\log_{10}$ transformation. In these cases the raw data is described by the median and interquartile range. Non-normal data sets were analysed by using Mann-Whitney and Kruskall-Wallis tests. All analyses were performed using the statistical programme Minitab 11.

The preference or avoidance of particular areas of the field was investigated using a preference index (Putman, 1986):-

$$\text{index} = \frac{\text{number of observations in area A}}{\text{surface area of A}} \times \frac{\text{total area surveyed}}{\text{total number of observations}}$$

Values greater than one indicate preference, values below one indicate avoidance.

4.4 RESULTS

4.4.1 DAILY TIME-BUDGETS IN WINTER AND SUMMER

The data (the number of scan sample observations) for each pony, were totalled over each of the three 24 hour periods (composite days) for each of the seven behaviour categories. The resulting data for the three composite days in winter and summer are presented in Tables 4.5 and 4.6.

Individual differences were investigated by using the most frequently observed behaviours, *ingestion*, and *resting* (the sum of *standing* and *lying*). There were no significant differences between ponies for *ingestion* or *resting* in either season ($P>0.05$; Friedman two-way analysis by ranks). Therefore, the daily behaviour in each season was calculated as a proportion of the total number of observations for all six ponies (total number of observations per category / 1728), and these proportions, as percentages, were used to represent the 24 hour time-budget of the ponies in winter and summer (Figures 4.4 and 4.5). The data in Figure 4.5 were corrected for missing observations as one 2 hour observation period for all 6 ponies was missed on day one and at a different time on day 3 (Appendix 4.3). The missing observations were distributed *pro rata* according to the proportion of observations in each category on the other two days.

Table 4.5; The behaviour of six Exmoor mares in the winter, presented as the total number of scan samples in seven categories of behaviour during three composite days.

		Behaviour category						
Pony	*Day*	*Ingest*	*Move*	*Stand*	*Lie*	*Interact*	*Other*	*Missing*
Beauty	1	64	1	15	4	0	0	12
	2	72	4	20	0	0	0	0
	3	74	2	10	0	0	2	8
	Total	210	7	45	4	0	2	20
Brandy	1	56	2	19	7	0	0	12
	2	67	0	20	8	1	0	0
	3	73	1	9	2	1	2	8
	Total	196	3	48	17	2	2	20
Browny	1	57	2	18	7	0	2	10
	2	68	2	18	7	0	1	0
	3	60	6	18	1	0	1	10
	Total	185	10	54	15	0	4	20
Friendly	1	59	1	17	8	0	1	10
	2	70	2	16	8	0	0	0
	3	66	1	13	4	0	0	12
	Total	195	4	46	20	0	1	22
Trim	1	61	1	19	6	0	0	9
	2	69	3	20	3	0	1	0
	3	59	1	20	3	0	1	12
	Total	189	5	59	12	0	2	21
Tufty	1	61	1	14	9	0	1	10
	2	70	1	19	6	0	0	0
	3	68	1	12	3	1	1	10
	Total	199	3	45	18	1	2	20
All*	Total	1174	32	297	86	3	13	123

Ingestion included 1 observation of drinking and 2 of eating nettle roots;
Moving included 1 observation of trot, the remainder were walk;
Other included 6 self groom, 4 investigating fence and 1 each of watching observer, stretch and flehmen.

* see Appendix 4.3 for corrections to seasonal total due to missed observations

Table 4.6; The behaviour of six Exmoor mares in the summer, presented as the total number of scan samples in seven categories of behaviour during three composite days.

		Behaviour category						
Pony	*Day*	*Ingest*	*Move*	*Stand*	*Lie*	*Interact*	*Other*	*Missing*
Beauty	**1**	**58**	**6**	**19**	**4**	**2**	**4**	**3**
	2	**44**	**6**	**43**	**1**	**0**	**2**	**0**
	3	**62**	**2**	**27**	**0**	**0**	**3**	**2**
	Total	**164**	**14**	**89**	**5**	**2**	**9**	**5**
Brandy	**1**	**63**	**7**	**14**	**2**	**2**	**5**	**3**
	2	**39**	**6**	**33**	**14**	**1**	**3**	**0**
	3	**54**	**2**	**28**	**5**	**2**	**3**	**2**
	Total	**156**	**15**	**75**	**21**	**5**	**11**	**5**
Browny	**1**	**59**	**6**	**16**	**4**	**3**	**3**	**5**
	2	**48**	**3**	**35**	**6**	**1**	**3**	**0**
	3	**62**	**5**	**22**	**1**	**2**	**2**	**2**
	Total	**169**	**14**	**73**	**11**	**6**	**8**	**7**
Friendly	**1**	**59**	**5**	**17**	**2**	**3**	**7**	**3**
	2	**47**	**7**	**22**	**15**	**1**	**4**	**0**
	3	**56**	**3**	**19**	**10**	**1**	**5**	**2**
	Total	**162**	**15**	**58**	**27**	**5**	**16**	**5**
Trim	**1**	**61**	**7**	**14**	**7**	**2**	**2**	**3**
	2	**46**	**7**	**31**	**8**	**0**	**4**	**0**
	3	**55**	**3**	**26**	**4**	**1**	**5**	**2**
	Total	**162**	**17**	**71**	**19**	**3**	**11**	**5**
Tufty	**1**	**58**	**6**	**19**	**3**	**4**	**3**	**3**
	2	**42**	**4**	**36**	**8**	**2**	**4**	**0**
	3	**57**	**1**	**23**	**3**	**4**	**6**	**2**
	Total	**157**	**11**	**78**	**14**	**10**	**13**	**5**
All	**Total**	**970**	**86**	**444**	**97**	**31**	**68**	**32**

Ingestion included 7 of drinking and 18 of eating sub-soil or mud;

Moving included 1 observation of trot, the remainder were walk;

Other included 20 self groom, 33 suckling, 8 watching observer, 5 urinating and 1 digging mud.

Figure 4.4; 24 hour time-budget (%) of Exmoor pony mares in winter.

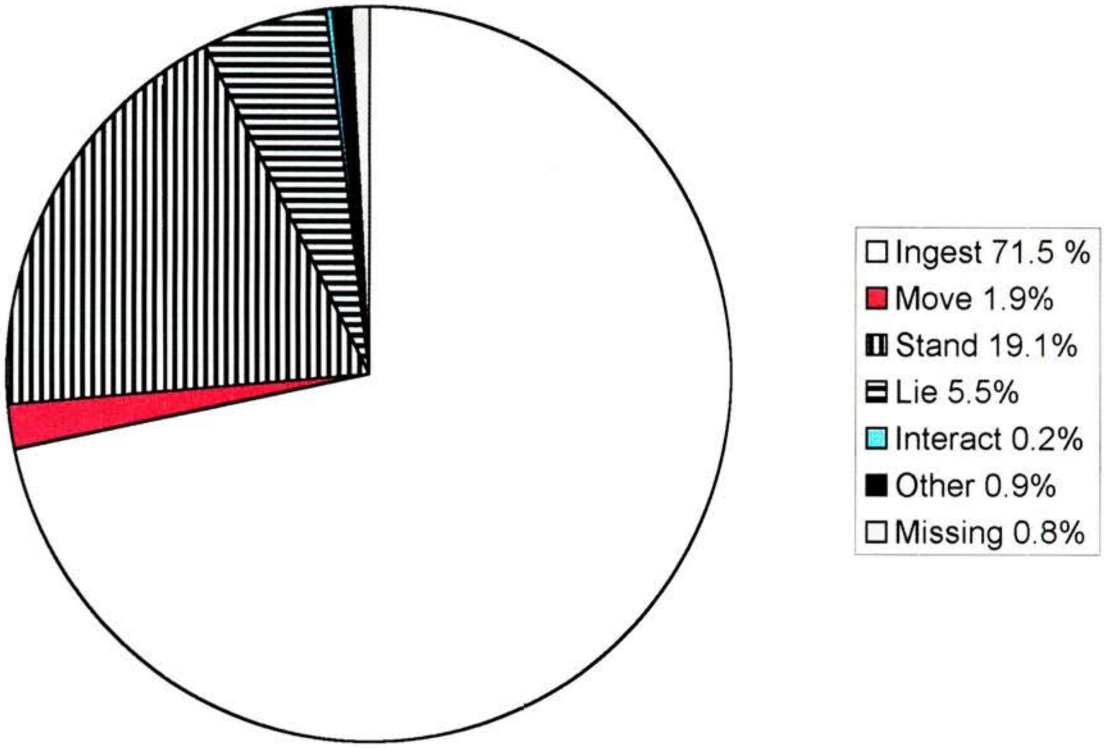
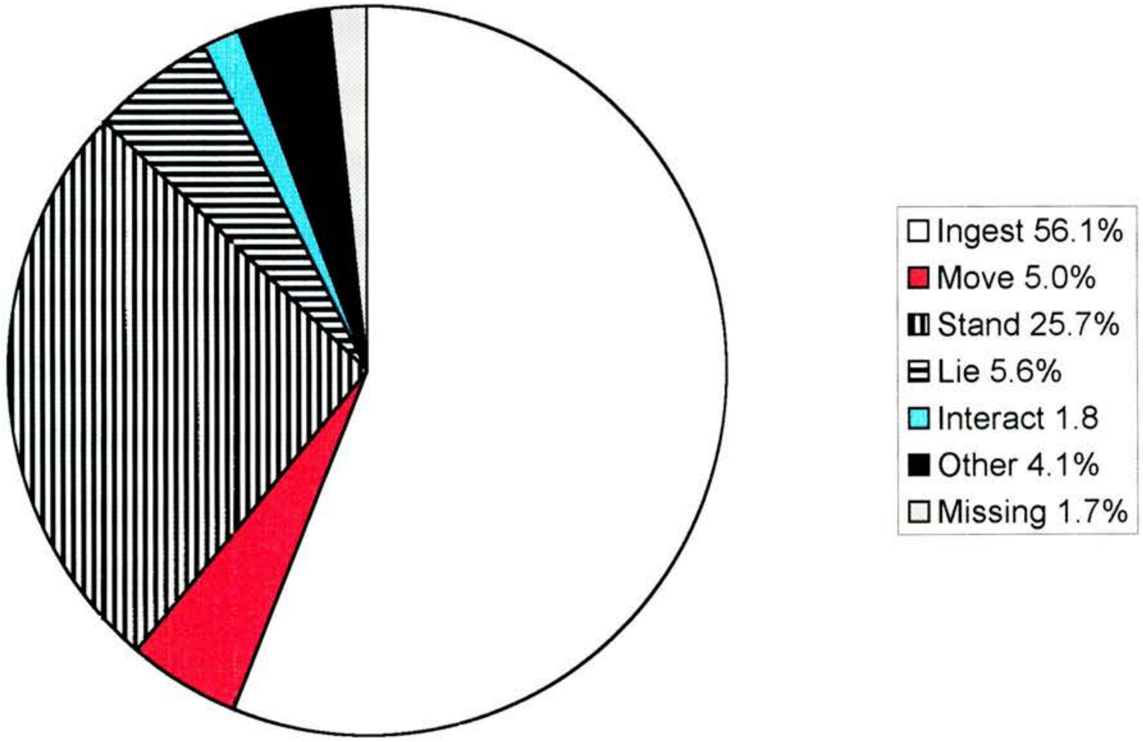


Figure 4.5; **24 hour time-budget (%) of Exmoor pony mares in summer.**



Seasonal differences in the proportion of each behaviour were investigated initially by using the seasonal totals of all seven behaviour categories (last line of Tables 4.5 and 4.6). The differences were significant (chi-square = 187.78, df = 6, $P<0.001$). The seasonal differences were then explored by making individual comparisons for each behaviour category by using the total data from each pony (last line for each pony in Tables 4.5 and 4.6) as a matched pair.

All categories except *lying* ($P=0.156$) showed significant seasonal differences. Total observations of *move*, *stand*, *interact* and *other* were greater in summer; total observations of *ingest,* and *missing* were greater in winter ($P<0.05$ in all cases; Wilcoxon signed rank test; one-tailed).

For both seasons, differences in behaviour between composite days were investigated using data from those categories with the largest number of observations; *ingesting* and *resting* (*standing* plus *lying*). In both winter and summer these differences were significant (Table 4.7).

Table 4.7; Differences in the total number of observations of *ingesting* and *resting* behaviour in six Exmoor mares in three composite days in winter and summer.

	Median number of observations		
Season / behaviour	*Day 1*	*Day 2*	*Day 3*
Winter *Ingesting*	59^{a}	69^{b}	66^{ab}
Resting	25^{ab}	25.5^{a}	17^{b}
Summer *Ingesting*	59^{a}	44^{b}	57.75^{ab}
Resting	21.5^{a}	42.8^{b}	27.7^{ab}

Different superscripts on the same row indicate significant differences ($P<0.05$; Friedman two-way analysis of variance by ranks).

4.4.2 THE SPEED OF TRAVEL, AND THE DISTANCES TRAVELLED DAILY

4.4.2.1 Speed of travel

The mares travelled more quickly whilst grazing or walking in winter compared to summer ($P<0.05$; Table 4.8).

Table 4.8; The speed of travel (m/s) of Exmoor ponies when grazing or walking in winter or summer, and when trotting or cantering in the summer.

Speed of travel (m/s)

Activity	*Grazing**		*Walking*		*Trotting*	*Cantering*
Season	winter	summer	winter	summer	summer	summer
mean			1.20^a	0.90^b	2.44	6.67
s.e.			0.031	0.076		
median	0.058^a	0.021^b				
Q1	0.026	0.015			min. 2.31	min. 4.61
Q3	0.074	0.029			max.2.56	max. 8.72
n	16	218	4	57	2	2

*The data for grazing were not normally distributed, therefore the median and interquartile ranges were calculated. Different superscripts in the same row indicate significant differences ($P<0.05$); grazing = Mann-Whitney test; walking = one way analysis of variance.

4.4.2.2 The distances travelled daily

Daily distances travelled between quadrat positions

The distances moved every two hours, as calculated by this method (4.3.3.6), and the daily totals are tabulated for each pony in Appendix 4.4. These include adjustments for missing values in the first and third composite days in the winter which were calculated as the average distance travelled for each pony in the equivalent time periods in the other two days.

The mean (s.e.) distance (m) travelled daily was calulated for the 18 daily total distances (3 days x 6 ponies) in both winter and summer. The daily distance travelled in winter, 3122.7 (188.36) m, was significantly less than the distance travelled in summer, 3749.0 (163.6) m ($P<0.05$). Within season there were significant differences in the distance travelled in each composite day (Table 4.9). In winter the distance travelled increased significantly each day ($P<0.05$), whereas in summer the longest distance was travelled on the first day, and the difference between days 2 and 3 was not significant ($P>0.05$).

Table 4.9; The mean (s.e.) distances (m) travelled daily by six Exmoor mares in winter and summer during each of three composite days.

	Mean (s.e.) distance (m) travelled daily	
Composite day	*Winter*	*Summer*
Day 1	2330.3^{a} (95.5)	4495.2^{a} (85.4)
Day 2	2974.6^{b} (96.9)	3127.0^{b} (121.0)
Day 3	4063.0^{c} (191.0)	3625.0^{b} (244.0)

Different superscripts within columns indicate significant differences ($P<0.05$).

Estimation of distance from the speed and duration of activities

In order to correct for *missing* observations, the seasonal occurrence of *ingesting* and *moving* were calculated as proportions of all observed behaviour, i.e. the total number of observations was equal to the total possible (1728) - the number *missing* (Tables 4.5 and 4.6). The speeds used were those in Table 4.8, for grazing and walking, as these were the predominant activities in *ingestion* and *moving*. The results were:-

Winter; grazing (3658.2) + walking (2073.6) = 5731.8 m / day
Summer; grazing (1034.2) + walking (3888.0) = 4922.2 m / day

4.4.3 BEHAVIOUR IN RELATION TO ENVIRONMENTAL CONDITIONS

4.4.3.1 Temporal patterns of behaviour

In winter the grazing periods were centred around dawn, midday, dusk and midnight. In summer there were two main periods, in the early morning and late afternoon / evening.

The frequency of *ingesting, moving, standing* and *lying* are presented for every 2 h of each of the three composite days in winter and summer in Appendix 4.5, with the concurrent records of dry bulb temperature, wind speed, presence of rain and biting flies. The complete weather records are summarised in Appendix 4.6.

Figure 4.6; Temporal activity pattern of six Exmoor pony mares in the winter.

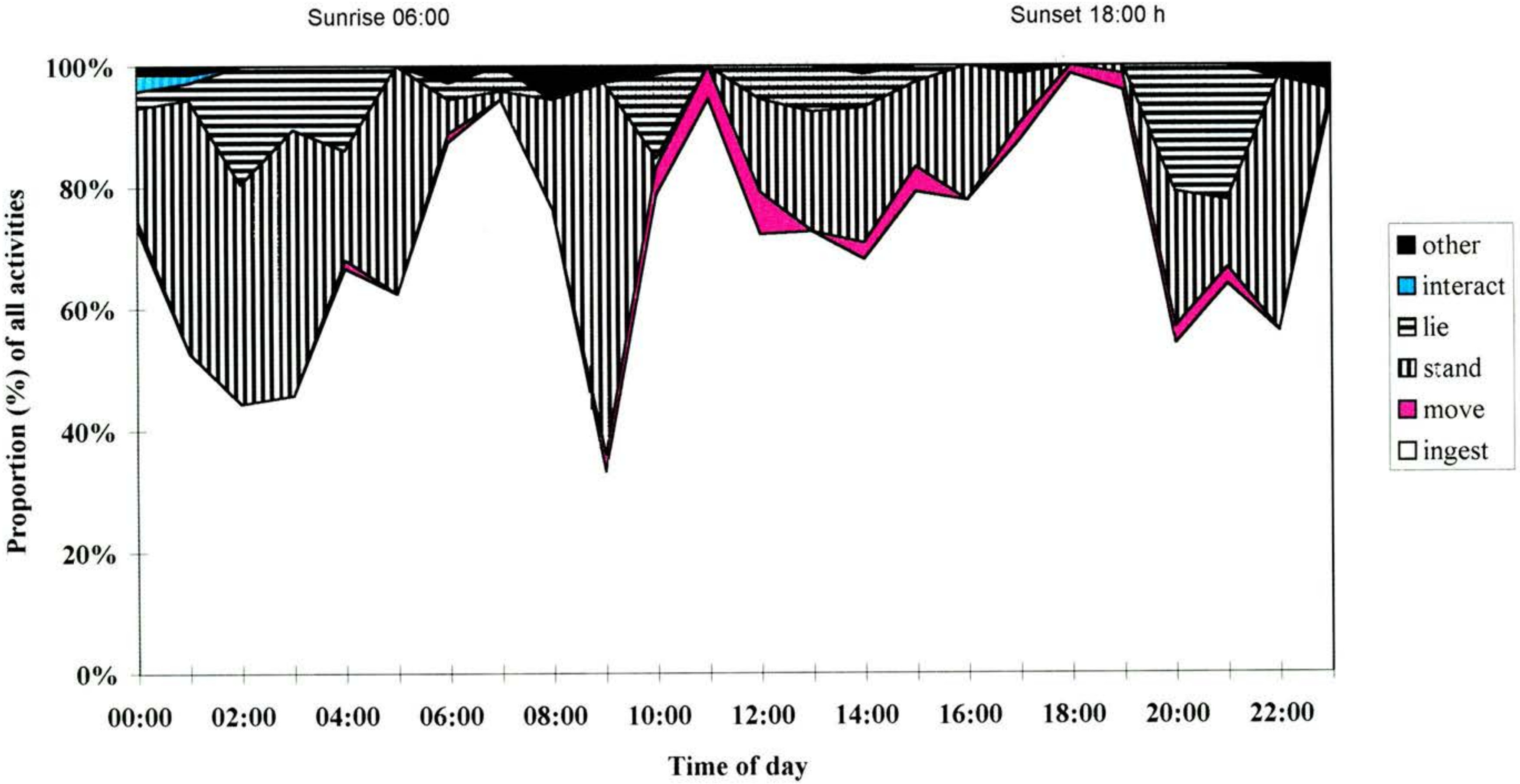
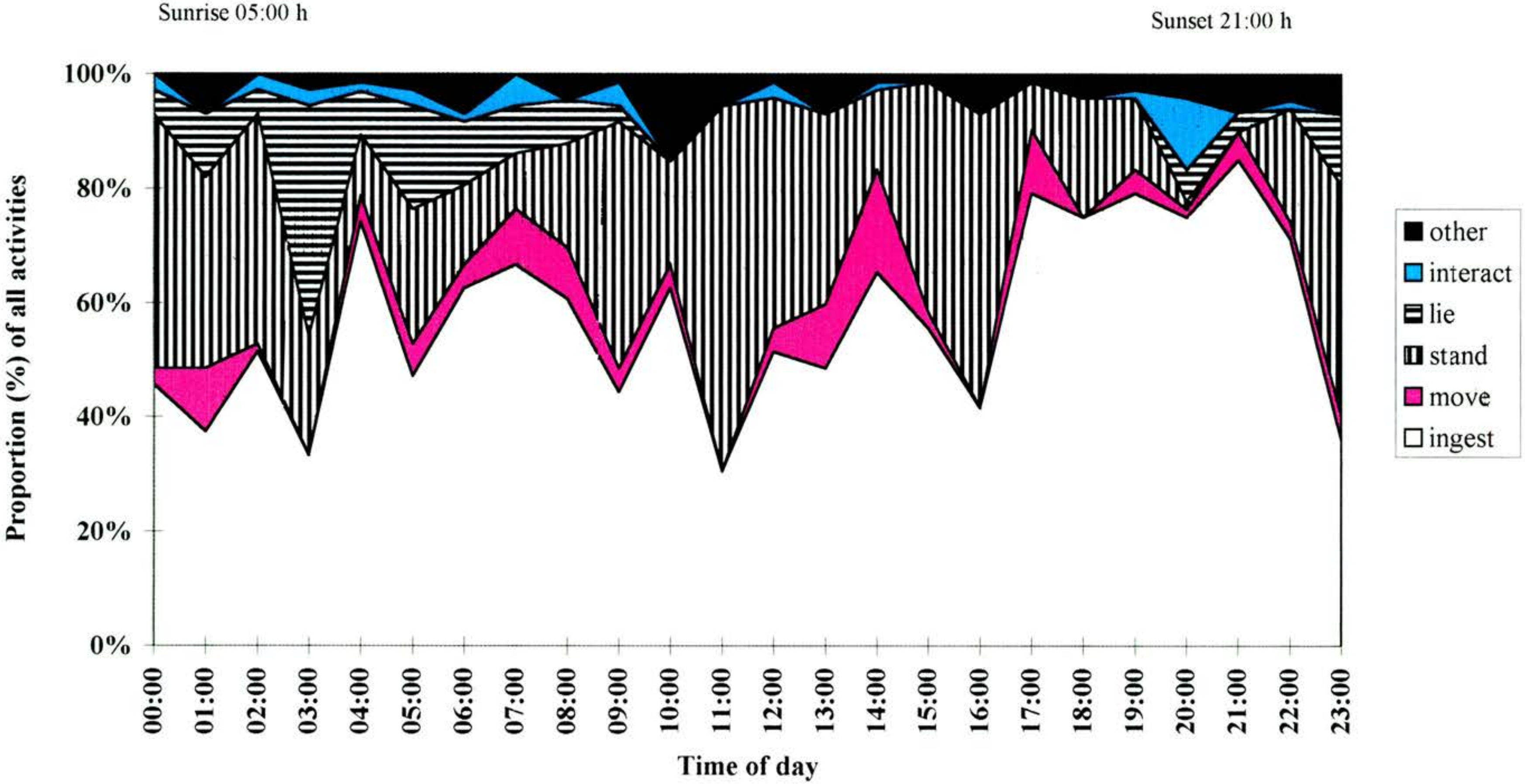


Figure 4.7; Temporal activity pattern of six Exmoor pony mares in the summer.



4.4.3.2 Preferred locations when resting (standing + lying)

No observations were recorded for D1, T7, Q2 or Q3 in winter (Table 4.10). Of the quadrats which were used, those preferred in winter were T1, B1, Q1, B4, D2, T5 and Q5 (Appendix 4.7).

Quadrat Q1 was the only area for which preference was also shown in the summer, the others being T4 (daylight only), T6 and B3. In summer, no observations were recorded for D1, D2, D3, D4, T5 and T7.

<u>Table 4.10</u>; Index* of preference (>1) and avoidance (<1) of areas of the field by ponies when *ingesting* and *resting* (*standing* + *lying*) during winter and summer.

	Index			
Behaviour	***Resting***		***Ingesting***	
Season	**Winter**	**Summer**	**Winter**	**Summer**
Quadrat				
D1	NR	NR	0.941	NR
D2	**4.049**	NR	**1.510**	0.051
D3	0.194	NR	0.888	NR
D4	0.408	NR	0.848	NR
T1	**2.212**	0.548	**1.961**	**1.077**
T2	0.654	0.401	**1.750**	**1.326**
T3	0.693	0.545	0.615	**2.036**
T4	0.181	**7.383**	0.814	**3.706**
T5	**1.043**	NR	0.961	0.412
T6	0.043	**2.926**	0.421	0.425
T7	NR	NR	0.117	0.035
Q1	**3.109**	**1.440**	**1.217**	**1.495**
Q2	NR	0.706	**1.597**	**2.667**
Q3	NR	0.674	0.429	**1.325**
Q4	0.136	0.128	0.592	0.340
Q5	**1.004**	0.193	0.941	0.297
B1	**6.315**	0.857	**2.371**	**1.161**
B2	0.181	0.308	0.733	0.558
B3	0.683	**1.812**	0.483	0.606
B4	**3.523**	0.108	0.850	0.363

* Putman (1986). NR = no observations of that behaviour were recorded.

4.4.3.3 Preferred locations when ingesting

All quadrats were used for ingestion in winter (Table 4.10), but the preferred locations were T1, Q1, B1, T2, Q2 and D2.

In summer T1, T2, T3, T4, Q1, Q2, Q3, and B1 were all preferred locations. No observations were recorded for D1, D3 and D4.

Therefore, areas preferred in the winter, except D2, were also preferred in the summer when preference was shown for a greater number of quadrats. The preferred quadrats in summer were also in the western part of the field. Some areas at the eastern end of the field were never used, and the remainder were "avoided".

4.4.3.4 Preferred locations when biting flies (*Tabanids*) were active

T4 was the only quadrat preferred when *Tabanids* were active; preference index = 13.6, but a stronger preference, index = 182.5, was shown for a localised area within T4, a patch of bare earth which had been the larger of the two dew ponds in winter.

Table 4.11; Data for calculation of the preference indices for quadrat T4 and an area of bare earth when *Tabanids* were active.

location	*area (m^2)*	*observations*
T4	10,000	143
bare earth	31.42	56
whole field	17,3651	1696

4.4.3.5 The difference between wind speed beside ponies in preferred standing and lying locations and the full speed of the wind

All the locations preferred during winter for standing or lying, except Q1, showed a significant reduction in wind speed beside the pony in comparison to full exposure to the prevailing wind (Table 4.12).

In summer there was a significant reduction in wind speed in Q1 ($P<0.05$), but no reduction in T4 where the majority of observations were recorded.

In order to compare seasons and locations on a common basis, only wind speeds measured when a south westerly wind was blowing were used in this analysis. (Figure 4.8; Appendix 4.6).

Table 4.12; The difference between the full speed of the wind (m/s) and the wind speed beside standing or lying ponies.

Median (Q1;Q3) wind speed (m/s)					
	Winter			*Summer*	
Quadrat (n)	**At pony**	**Full speed**	***Quadrat (n)***	**At pony**	**Full speed**
D2 (33)	**2.0^{a} (2;4)**	**7.0^{b} (7 - 10)**			
T5 (12)	**6.0^{c} (6;6)**	**11.0^{d} (11;11)**			
B4 (14)	**2.0^{a} (2;2)**	**6.0^{b} (6;6)**			
Q5 (6)	**6.0^{e} (6;6)**	**10.0^{f} (9.25;10)**			
T1 (46)	**2.0^{a} (1;2)**	**5.0^{b} (5;6)**			
Q1 (4)	**1.0 (1;3.25)**	**4.0 (4;4)**	**Q1 (16)**	**1.0^{c} (1;3)**	**3.0^{d}(3;3)**
B1 (4)	**1.0^{a} (1;1)**	**4.0^{b} (2.5;4)**			
			T4 (79)	**2.0 (2;3)**	**2.0 (2;3)**

(n) = number of observations

Different superscripts within the same row and the same season indicate significant differences; ab = $P<0.001$;cd = $P<0.01$; ef = $P<0.05$ (Wilcoxon signed rank test).

4.4.3.6 Influence of wind speed on orientation of mares to the wind whilst grazing

Hindquarters to the wind was the most frequent orientation of ponies when grazing in the winter (Figure 4.9). Over all wind speeds in winter, sideways = 13.1 %, facing = 34.5 % and hindquarters = 53.5 % of all observations. If there was no relationship between wind speed and the orientation of mares in relation to the direction of the wind then it could be expected that 50 % of observations would be classed as side to the wind (left or right), 25 % classed as facing the wind and 25 % as hindquarters to the wind.

As wind speed increased in summer (Figure 4.10) hindquarters and facing the wind were increasingly preferred over side to the wind.

The observations presented as percentage points in Figures 4.9 and 4.10 are in Appendix 4.8.

Figure 4.8; The duration (hours) of winds from different directions (blowing from the periphery to the convergent point) in winter and summer.

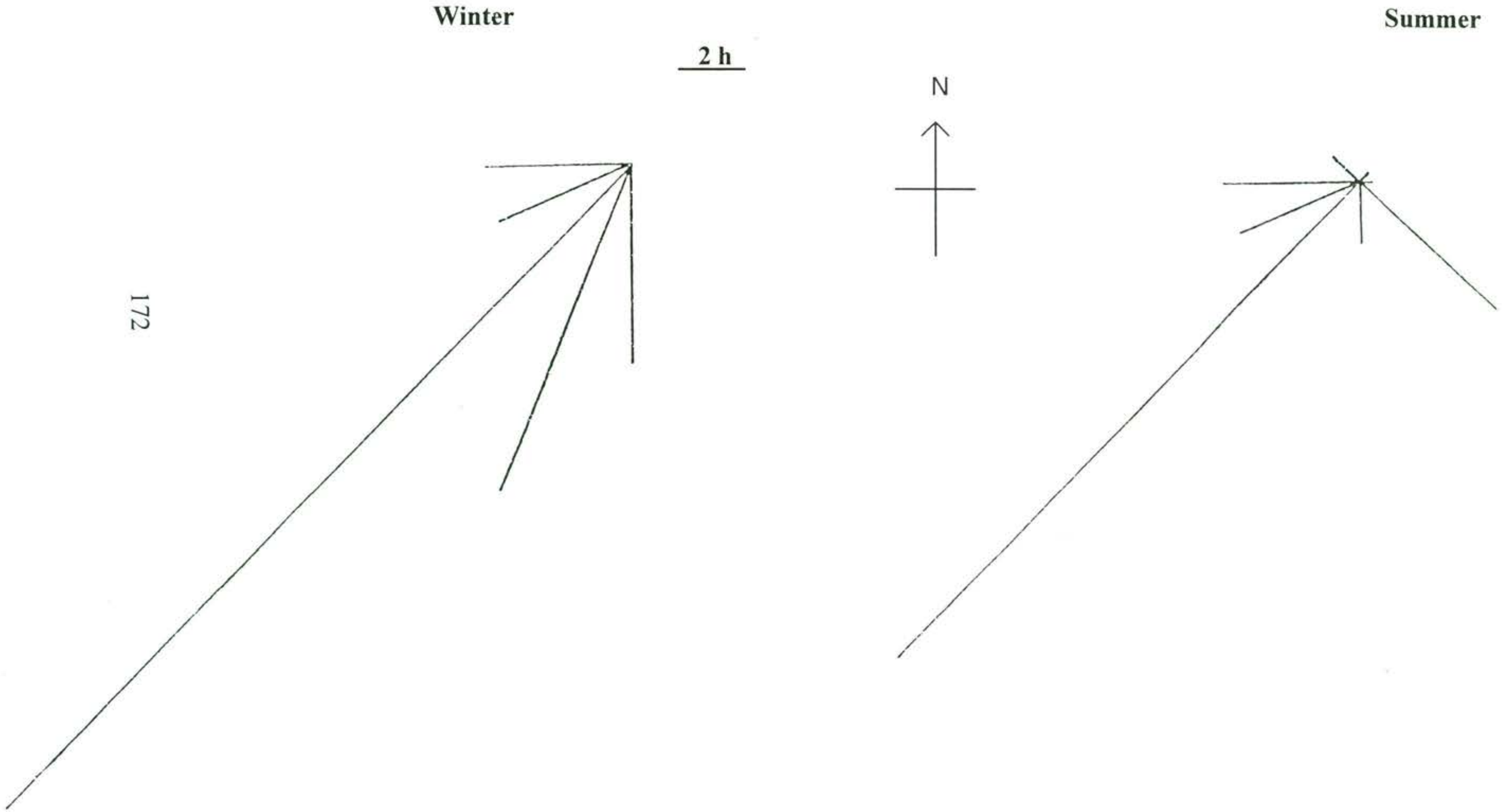


Figure 4.9; **Relationship between wind speed (m/s) and the orientation; hindquarters, side or face to the wind, of mares grazing in the winter.**

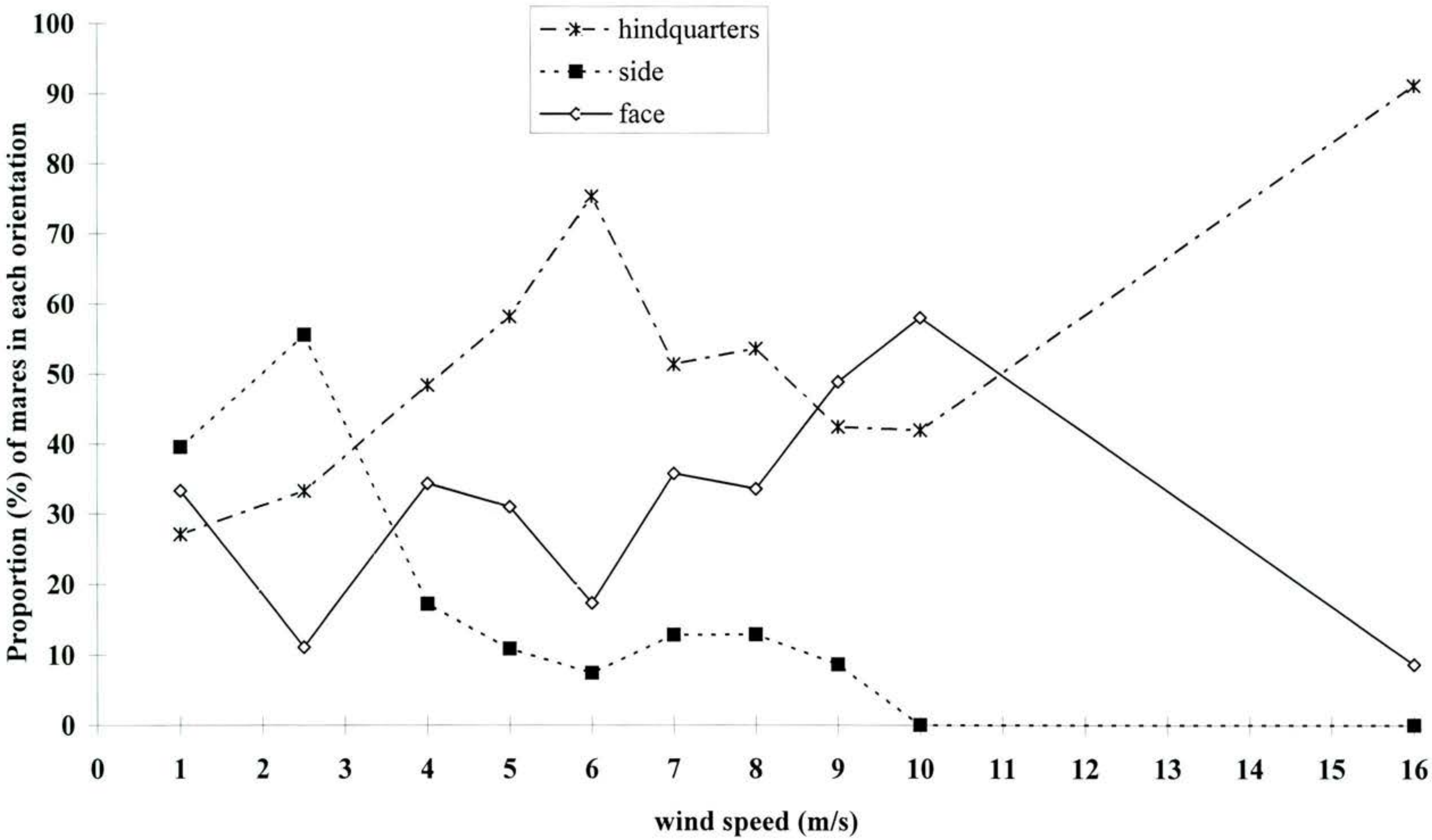
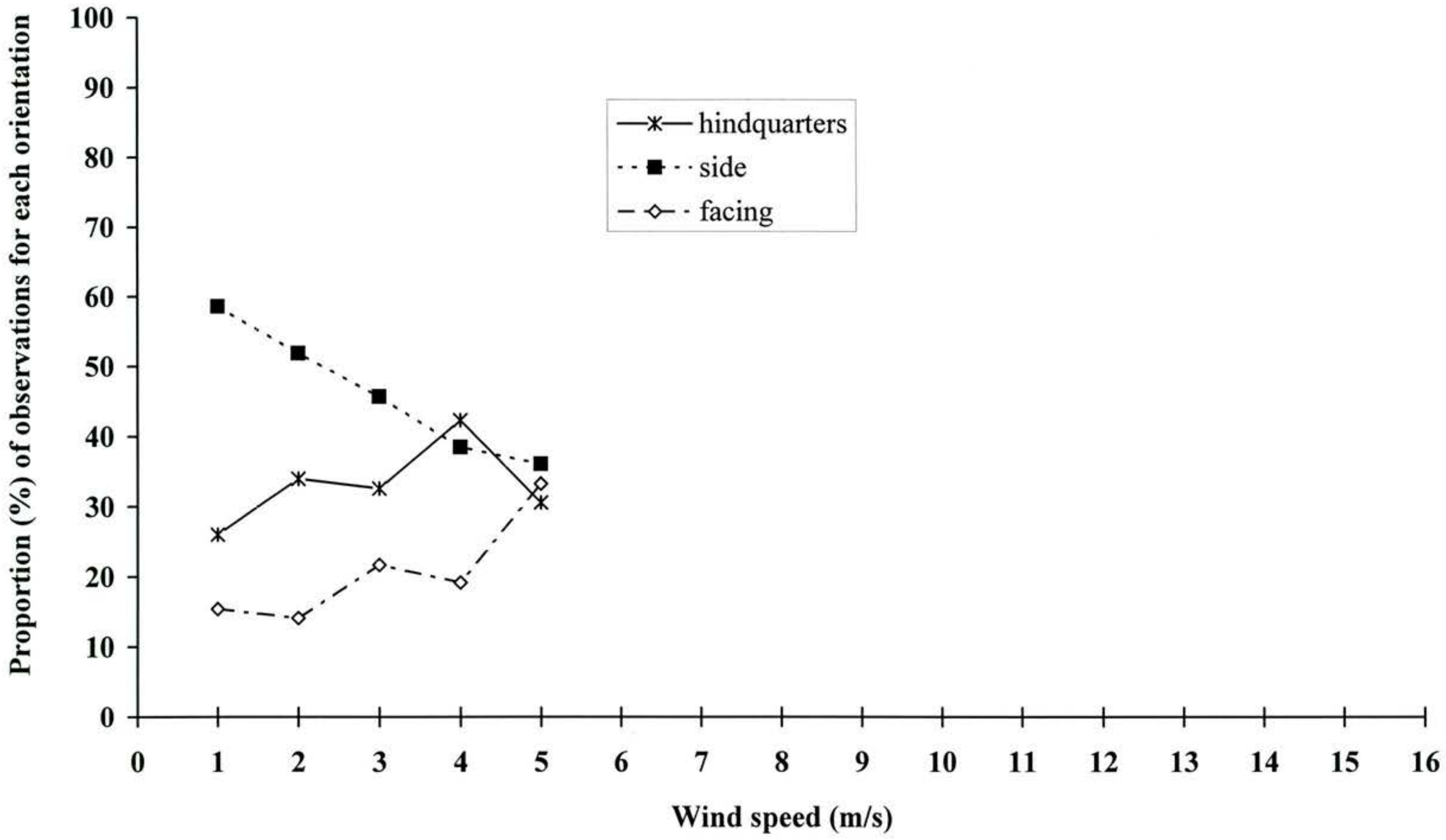


Figure 4.10; **Relationship between wind speed (m/s) and the orientation; hindquarters, side or face to the wind, of mares grazing in summer.**



4.4.4 GRASS LENGTH AND GRAZING BEHAVIOUR

Drinking and eating soil or roots accounted for less than 2.6% of all *ingesting* observations in winter or summer. Therefore the term *grazing* will be used instead of *ingesting*.

4.4.4.1 Grass length

The grass lengths in those quadrats measured in both seasons (T1-4, Q1, Q3 and B1-3) were all significantly shorter in the winter (Appendix 4.9).

Grass lengths were classified according to the uniform areas of summer sward (Table 4.13) described as *short* (lawns), *average*, *long* (roughs) and *in rushes*.

Table 4.13; Grass lengths (mm) in uniform areas of sward in the summer.

	Grass length (mm)			
Classification	*mean (s.e.)*	*median*	*Q1*	*Q3*
Short		32.5	30.0	39.4
Average	92.6 (3.41)			
Long	171.1 (5.82)			
In rushes	240.3 (7.41)			

The height of the winter sward in quadrats T1, Q1 and B1-3 was not significantly different from *short*. In all other quadrats measured, grass heights were also significantly less than *average* ($P<0.05$).

In summer the grass in all quadrats, except five, were not significantly different from average ($P<0.05$). B1 had *short* grass, T1, T6 and T7 all had *long* grass whilst D4 had grass which was not significantly different from either *long* or grass *in rushes*.

4.4.4.2 Grass length in preferred grazing areas

The general sward in the quadrats preferred for grazing could be described as being short in the winter and of average length in the summer. The grass lengths in those quadrats preferred for grazing are described in Table 4.14.

The height of the winter sward in quadrats T1, Q1 and B1 was not significantly different from the height of the *short* summer sward ($P<0.05$). In all other quadrats, grass lengths were significantly longer, but not as long as the *average* summer sward ($P<0.05$).

Quadrat B1 had grass which was significantly longer than the *short* summer sward, but not as long as the *average* sward ($P<0.05$). All other swards were not significantly different from *average* length ($P>0.05$).

Table 4.14; Grass lengths (mm) in quadrats preferred for grazing in winter and summer.

			Grass length (mm)		
Season / Quadrat		*mean (s.e.)*	*median*	*Q1*	*Q3*
Winter	T1	33.3 (2.58)			
	T2		40.0	30.0	50.0
	Q1		36.3	30.0	53.8
	Q2	52.1 (4.04)			
	B1	44.6 (3.54)			
Summer	T1	148.4 (7.52)			
	T2	129.3 (9.34)			
	T3		87.5	72.5	128.8
	T4	77.8 (5.16)			
	Q1		68.8	57.5	101.3
	Q3	122.0 (8.53)			
	B1		55.0	38.8	76.9

4.4.4.3 Grazing behaviour

When all measurements of grazing behaviour in the winter were compared to all those made in the summer, regardless of sward classification (Table 4.15), bite rate, step rate and speed were all significantly greater in the winter. The bite:step ratio was smaller in the winter, but there was no significant seasonal difference in step length.

Bite rate increased significantly ($P<0.05$) as grass length decreased from *long* to *average*, but there was no significant difference in bite rate between *average* and *short* summer swards. The winter bite rate was significantly faster than that on the *average* summer sward, but not the *short* summer sward.

Step rate was faster in the winter than on any sward classification in the summer ($P<0.001$), between which there were no significant differences ($P>0.05$). Not surprisingly, the same relationships existed for speed ($P<0.001$).

The bite:step ratio on the *short* and *average* summer swards was significantly greater ($P<0.05$) than that measured in the winter. The bite:step ratio on the *long* sward was not significantly different from either the *short* or *average* swards, or that recorded in the winter.

Table 4.15; Comparison of different measures of grazing behaviour in pony mares on different swards in winter and summer.

Mean (s.e.)* Median (Q1;Q3)

measurement	***winter***	***summer***			
		all data	short	average	long
bite rate (bites/min)	**61.44^{a1}** **(1.54)** **n=89**	52.42^{2} (45.0;60.71) n=261	**55.79^{ab}** **(1.98)** **n=46**	**51.82^{b}** **(1.30)** **n=59**	**40.74^{c}** **(2.84)** **n=17**
step rate (steps/min)	6.67^{a1} (5.06;9.42) n=89	4.25^{2} (3.08;5.83) n=261	4.36^{b} (2.96;6.18) n=46	4.50^{b} (3.40;6.00) n=59	3.58^{b} (2.14;5.74) n=17
bite:step ratio	10.04^{ax} (6.11;12.55) n=89	12.0^{b} (9.06;17.0) n=261	12.43^{y} (9.22;17.0) n=46	11.25^{y} (8.50;16.43) n=59	**12.58^{xy}** **(1.43)** **n=17**
speed (m/s)	0.058^{a1} (0.026;0.074) n=16	0.021^{2} (0.015;0.029) n=218	0.02^{b} (0.014;0.029) n=32	0.021^{b} (0.013;0.028) n=49	0.016^{b**} (0.015;0.030) n=9
step length (m)	0.36 (0.27;0.45) n=16	0.32 (0.23;0.40) n=218	0.26 (0.21;0.32) n=32	**0.29** **(0.015)** **n=49**	**0.42** **(0.061)** **n=9**

* presented for normally distributed sets of raw data.

Different superscripts in the same row indicate significant differences ($P<0.05$); superscripts a,b,c; x,y; indicate the result of an analysis of variance. Where median values are given, the test was run on $\log_{10}$ transformed data. Numerical superscripts indicate the results of a Mann Whitney test.

** The speed of grazing on average and long grass was compared using a Mann-Whitney test.

4.5 DISCUSSION

The 24 hour time-budgets of the Exmoor mares in this study were similar, in both winter and summer, to those reported for other free-living horses (Duncan, 1983; Pratt et al., 1986), although there were some differences. The proportion of 24 hours spent feeding by the Exmoor mares in winter (71 %) was similar to that described for New Forest ponies (~ 80 %) by Pratt, et al. (1986), but the summer proportions were different. The Exmoors grazed for 56 % of 24 hours whilst the New Forest ponies averaged ~75 % in the summer. Other horses living in wooded areas also spent between 70 - 80 % of their time feeding in the summer (Kownacki et al., 1978; Salter and Hudson, 1979; Kaseda, 1983a), whereas horses in the more open areas such as the Camargue spent about 60 - 65 % of their time feeding (Duncan, 1980).

The seasonal variation in daily grazing time in the populations of horses mentioned above varied by 5 - 10 % which was less than the 14 % change seen in the Exmoor mares. Differences in forage availability and quality during the summer could be relevant. Forage availability for preferential grazers such as horses may be lower in woodland, where the relative stocking density on the available grassland may be higher (Kownacki et al., 1978; Salter and Hudson, 1979; Kaseda, 1983a), than on hill pastures (this study) which would partly explain the differences seen in summer. According to Klimov's (1988) observations, various environmental factors may interact, for instance horses which normally rest during periods of high ambient temperature may continue to graze if forage availability is low even if temperatures are as high as usual. Therefore, when such information is available, the climatic and nutritional conditions need to be considered when comparing the behaviour of different populations of horses.

Mayes and Duncan (1986) suggest that the basic requirement for rest, particularly paradoxical sleep (Belling, 1990), is an important factor determining the temporal and daily feeding patterns of horses. The resting theory was supported by Duncan's (1980) observations that stallions decreased their feeding time rather than their resting time when they were more active in getting and keeping mares. The results for the Exmoor mares also agreed with this theory as there was no seasonal difference in the time spent lying down. However, there was an increase in standing behaviour in summer (Figures 4.4 and 4.5). From the observed preference of the Exmoor mares for standing in an exposed location (T4) during the day in summer, this seasonal increase in standing, and decrease in grazing time, may be attributed to a combination of heat stress and attacks by blood-sucking *Tabanids* (Figure 4.7; Appendix 4.5). The same conclusions have been drawn by others from similar observations (Tyler, 1972; Mayes and Duncan, 1986).

The preferred standing location, a patch of bare earth in quadrat T4, the highest, level part of the field, was exposed to all winds except those from the north. Shade was not available to these Exmoor ponies, and this location offered the best opportunity for evaporative heat loss. Respiratory rates from 45 to 100 breaths / min (normal is ~12 breaths/min; Hayes, 1987) were recorded from two Exmoors which had been standing still in this location for at least half an hour (shade temperatures of 16 - 22 °C with no measurable wind speed). Clayton (1992) describes nasal panting as a thermoregulatory mechanism used by horses after exercise, but elevated respiration rates have not been reported for free-living horses. Other possible reasons for elevated respiratory rates, such as clinical illness, were not obvious from direct observations of behaviour although they cannot be ruled out on the basis of these observations alone.

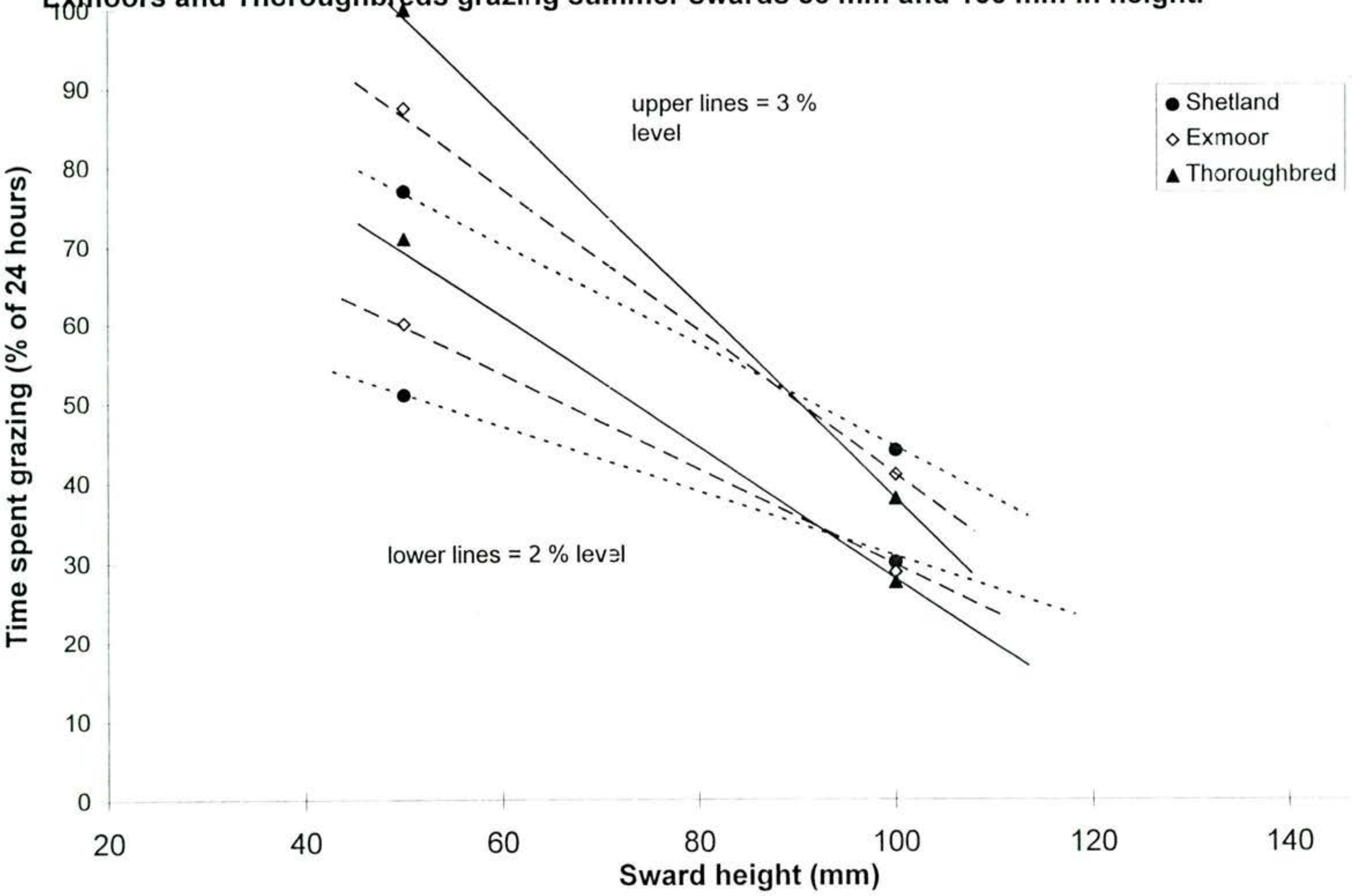
A strong preference for the bare patch of earth in T4 was evident when *Tabanids* were active. Other horses have shown the same preference (Tyler, 1972; Klimov, 1988) and so have reindeer (Helle and Aspi, 1984). In the middle of the day, bare earth or sand may be hotter than the surrounding herbage and create rising air currents which may carry exhaled CO_2, a strong fly attractant, away from the ground surface and make it more difficult for the low-flying *Tabanids* to find their hosts (Helle and Aspi, 1984).

Tabanids are associated with damp areas (Chinery, 1984), and were plentiful in the eastern end of the field which was dominated by *Juncus spp.* (rushes). This partly explains why the Exmoors did not use the areas in the east of the field during the day in summer, but did use them at night. Night-time use was almost exclusively restricted to resting (Table 4.10) in the shelter of the southern boundary wall (T6), with mares grazing their way through T6 as they moved to the west of the field during the dawn feeding period. Other areas used for resting were B3, also beside the wall, and Q1 near the water trough. Water and shelter have both been associated with resting areas of other free-living horses. New Forest ponies moved from grazing areas into woodland at dusk at all times of the year (Pratt et al., 1986), and feral horses in the U.S.A., which only drank at night in summer, stayed close to the water holes until resuming feeding in the early morning (Pellegrini, 1971).

In winter, differences between the wind speed measured at the pony and in the full force of the wind indicated that the mares used their preferred resting locations because of the shelter available in them (Table 4.10; Figure 4.2). All the preferred locations had areas that were sheltered from the prevailing winds by either topographical or man-made structures (Figure 4.1). Most measures in winter were made in D2 (mostly Drybank Hole) and T1 (close to the high western wall), where the difference between the wind speeds at the pony and the full wind speed (median values) was 2 - 7 m/s in D2, and 2 - 5 m/s in T1 (Table 4.12). Using the median winter temperature (5 ^{0}C; Appendix 4.6), and the tables of Effective Ambient Temperature (EAT) developed for cattle by Ames and Insley (1975) the locations used by ponies increased EAT from -4 ^{0}C (D2) and -2 ^{0}C (T1) to +1 ^{0}C. This sheltering behaviour is usual in free-living horses (Tyler, 1972; Welsh, 1975; Pratt et al., 1986; Albiston, 1987), and is thought to be important in energy conservation (Kaseda, 1983a; Berger, 1986) as it reduces the rate of heat loss from the animal by forced convection (McArthur, 1981; Blaxter, 1989). The relationship between wind speed and convective heat loss has not been established for horses and would of course vary with the density of the hair coat (McArthur, 1981).

The tendancy for the Exmoor mares to rest (~ 66 %) more than graze (~ 33 %) at 09:00 h in the winter was also reported for feral horses in a Canadian winter, which rested around 10:00 h (Salter and Hudson, 1979). As Tyler (1972) noticed that New Forest ponies increased their time standing still when the sun shone in winter, sunshine may have been a factor contributing to the 09:00 rest period. However, this only occurred in one of the three observations periods which made up the final proportions displayed in Figure 4.6. On that day the ponies stood one behind the other close beside, and parallel to the stone wall in B3/4. They were sheltered there from a cool breeze (5 ^{o}C, 6 m/s), but also had the sun on their backs. Apart from the sunshine, conditions were similar when they grazed at this time (6 ^{o}C, 6 m/s). On the other day when they

Figure 4.11; **Predicted grazing time (% of 24 hours) required to harvest daily maintenance requirements, based on dry matter intakes of 2 % and 3 % of body weight, for Shetlands, Exmoors and Thoroughbreds grazing summer swards 50 mm and 100 mm in height.**



rested, the sky was overcast and they were standing out of the wind in Drybank Hole (10.5 °C, 10 m/s).

This break in feeding may have been related to the animals being satiated after the dawn feeding period. The time it takes a grazing animal to harvest the amount of food required to reach satiety depends partly on the height and density of the sward in relation to the width of the incisor arcade (Illius and Gordon, 1988). It has been suggested that horses maintain their rate of intake by increasing bite rate on shorter swards, and Pollock (1980) found a negative correlation beween grass height and bite rate. However, this will only maintain intake rates within a certain range of sward height, after which grazing time would have to increase as sward height decreased.

Myers (1994) investigated this relationship for small (Shetland ponies) and large (Thoroughbred) horses by measuring bite rates and bite sizes on summer swards of different heights, and estimating the time it would take for these horses to harvest dry matter (DM) intakes equivalent to 2 % and 3 % of body weight. The DM intakes were based on the published maintenance requirements of adult (2 %) and immature, growing horses (3 %; NRC, 1989). The grass heights and bite rates on which Myers (1994) based her calculations were very similar to those measured in this study of Exmoor mares. The incisor arcade of Exmoor ponies (6.87 cm), as measured by Sutters (1994) in a comparative study of six breeds of horse, lay between those of Shetlands (6.16 cm) and Thoroughbreds (6.97 cm). The theoretical position of Exmoor ponies in relation to the intake rates of Shetlands and Thoroughbreds estimated by Myers (1994), is presented in Figure 4.11. The lines for the Exmoors should perhaps be closer to the Shetlands than the Thoroughbreds on the basis that their body weight is only about 100 kg greater than a mature Shetland, but 200 kg less than an average Thoroughbred (550 kg).

Whilst these estimations do not take into consideration many other factors which would influence DM intake, such as sward density, palatability or fibre content, they do serve to show that horses with a smaller body weight are at an advantage on shorter swards. However, when maintenance energy requirements are high due to growth or lactation the graph also illustrates that even smaller horses would not be able to harvest all their daily requirements on short swards unless they grazed for 90 % of 24 hours.

This explains why the New Forest ponies also graze on other plant communities as well as the short, preferred grasses. It also explains Klimov's (1988) comment that when horses are seen to graze under unusual conditions, such as the midday heat, that they are approaching the point when their grazing needs to be supplemented with additional fodder.

The sward heights reported for the favoured grazing areas of the New Forest indicate a height of <20 mm in the summer with a range of bite rates from 72 - 43 / min (Table 4.2; Putman, 1986). The highest rate was recorded in May when the grass began to regrow and is presumably highly palatable, but has not reached its greatest density suggesting that bite size will still be small. In comparison to the bite rates reported for the New Forest ponies, the Exmoor mares had an average bite rate of 55.8 bites/min (Table 4.15) on a short sward averaging 32.5 mm (Table 4.13). Putman (1986) suggested that the lower bite rate seen on very short swards could also be due to the ponies being increasingly selective in their choice of food, as was seen to a greater extent on *Molinia* as it became increasingly unpalatable, and to an extreme when browsing gorse (Table 4.2). The bite rates of the Exmoor mares when grazing in areas of long grass (>170 mm), 40.74 bites/min, were comparable to figures of 44 bites/min (Putman, 1986) for ponies grazing *Molinia* (30 - 130 mm; Robertson, 1984), but were not as low as the bite rates of 24 - 28 bites/min reported for horses eating grass >100 mm in height (McCracken, 1992).

The relative maturity of the long grasses and the speed at which the horses moved through these areas, which may have been used as latrines, may relate to the variation in bite rate recorded in the different studies. However, McCracken (1992) did not find any significant differences between the step rates on grass of different heights; 4.4 steps/min (<50 mm); 3.7 steps/min (50 - 100 mm), 4.7 steps/min (>100 mm). Her study was made in the summer with riding horses whose step rates were very similar to those of the smaller Exmoors which ranged from 3.58 - 4.5 steps/min in the same season, and which also did not differ significantly on swards of differing length (Table 4.15; $P>0.05$). Neither the grazing speed (0.016 - 0.021 m/s) nor the step length (0.26 - 0.42 m) of the Exmoors varied significantly on different summer swards.

Seasonal variation was evident in the step rate of the Exmoor mares, with a significant increase from 4.25 steps/min for all grass types in the summer to 6.67 steps/min in winter ($P<0.05$). The winter sward height was shorter than the summer sward, ranging in the preferred quadrats from 33 - 52 mm. Winter grazing behaviour was different to that seen in the summer in several ways. Bite rate (61 bites/min) was similar to that on the short summer sward, but was significantly faster ($P<0.05$) than the average for all summer observations (52 bites/min). The median travelling speed increased from 0.02 m/s in summer to 0.058 m/s in winter which relates to the significant increase in step rate ($P<0.05$). However, the fact that changes in speed and step rate were not of the same magnitude and step length remained constant may be a consequence of the large differences in sample size. The seasonal changes in bite rate and grazing speed were reflected in a significant decrease in the bite:step ratio from around 12:1 in summer to 10:1 in winter ($P<0.05$). The energy costs of grazing have been found to increase in cattle as grazing intensity increased i.e. bite rate increased (di Marco, Aello and Mendez, 1996). The changes in grazing behaviour of the Exmoor mares suggest, therefore, that their energy costs of grazing would increase in the winter. Very few observations of trot and canter were recorded so calculations of the energy costs of locomotion in free-living horses can be estimated on the basis of the energy costs of walking over different ground surfaces. During the gathering of ponies the faster gaits are used and will increase the energy costs of that day's activity. However, these costs will vary as the speeds used and distances covered depend on the terrain crossed and the location of holding facilities in relation to the home-range of the ponies.

The increase in duration of feeding and in bite rate in the Exmoor mares probably reflect a decrease in forage quality and may indicate a decrease in quantity which is also suggested by the shorter sward heights per quadrat (Table 4.14). A decrease in selectivity is also suggested by the increase in bite rate and also by the mares using all areas of the field for grazing in winter in contrast to the summer. The eastern end of the field was relatively sheltered from the prevailing south westerly winds which, along with the lack of *Tabanids* in winter, explains the seasonal differences in the use of this area.

The fact that horses prefer to stand with their hindquarters to the wind is widely known (Arnold and Dudzinsky, 1978) so the general orientation of the ponies in relation to the direction of the wind in winter was as expected (Figure 4.9). Duncan's (1983) observation that horses faces seemed to be particularly sensitive to the wind seems at odds with the increase in the proportion of animals facing the wind between 8 and 12 m/s in Figure 4.9, however, as the prevailing wind was from the southwest, and the preferred resting areas were in the south and west of the field, animals would have had to move into the wind to reach their resting areas. When this behaviour was investigated in summer (Figure 4.10) there was still an overall preference for hindquarters or face to the wind. The change from the random relationship between the three orientations when wind speeds were just registering on the anemometer (1 m/s), to the preference shown at 5 m/s may have been related to day and night time grazing as the mares still chose sheltered areas for resting at night.

As in other horses, the Exmoor mares used tracks when walking between locations, particularly to water in the summer (Pollock, 1980). They also used soil licks, eating sub-soil along fence lines, in the quarry, and from the dried dew ponds in T4 (the bare earth) and the muddy remains of another seasonal pond in B1. Fresh top-soil was readily available as mole hills, but the mares were never seen to eat this. Soil was not eaten during the winter, but the water which collected over the soil-lick sites was drunk, plus other surface water, to the total exclusion of water from the trough. As the opposite was true in the summer there may have been minerals available in solution in the surface water which were also available in the soil at these sites, but not available in the trough water. However, this is conjecture and needs a specific study.

Unlike the horses seen rolling in the wet mud surrounding water holes (Feist and McCullough, 1976), the mares used the dry dust in T4 for rolling in summer and mole hills in the winter. Dry, fine soil is the usual choice in horses (Pellegrini, 1971) and the Exmoors only became coated in mud if they rolled in the dust when they were wet after rain.

The total daily distances moved by the Exmoor mares ranged, according to the two methods of estimation, from 3.12 - 5.7 km/day in the winter; and from 3.75 - 4.92 km/day in the summer (4.4.2.2). Both lower estimates were calculated using the quadrat locations within a two hour period of observation as the basic unit of measure, whilst the larger distances were based on the speed and duration of grazing and moving behaviour (walking) in each season.

The errors related to the quadrat method varied depending on the number of new quadrats entered between each 15 min scan. Assuming that the maximum error would be equivalent to the diagonal distance from one corner of the 100 m square to the other, this would equal a distance of ±141.4 m. Under certain conditions the tendency was probably to underestimate. If ponies centred their movements around a particular quadrat e.g. T4 in summer, they may never have been recorded outside the quadrat during the two hour period so a zero distance would be recorded. Another time when underestimation was possible was if an animal moved e.g. to the water trough from T4, and was returning to T4 when the next location was recorded. In practice the assumption made during calculations, that the animal was in the centre of the square, and the ease with which quadrat boundaries were identified, may have halved the error to ±70.7 m i.e. the distance from the furthest point on the boundary to the centre of the square.

The second method used the proportion of 24 hours spent in mobile activities, grazing and walking, multiplied by the estimated speeds of these activities. Whilst the method of estimating distance (pacing it out) did not change between seasons, giving a constant error factor, the number of observations in winter was low, particularly for the speed of walking. A larger error may have come from an overestimation of the time spent walking as a consequence of the 15 min time interval used for the scan samples because periods of walking in horses are short in relation to the scan interval (Mayes and Duncan, 1986). However, walking periods whilst grazing are also relatively frequent so their number may be underestimated, cancelling out the overestimation due to their brevity.

The Exmoor mares spent 5 % of the day moving in summer and 2 % in the winter in comparison to the Camargue mares which spent 9 - 10 % of the day moving in spring/summer and 5 - 6 % in the other two seasons (Duncan, 1980). This seems to suggest underestimation, but the Camargue mares ranged over a much larger area than the Exmoors, and were in a situation where competing stallions may have herded them whereas the Exmoors were isolated from such disturbance and were never observed to be herded by the stallion during 140 hours of observation.

Without a control measure of the actual distance moved by the mares (distance wheel, trailing cotton etc. which were not an option in this study) the relative accuracy of the two methods cannot be assessed. On the basis that the quadrat method has been used under similar circumstances (Pollock,1980) and that the estimated distances fall within the range of the few other estimates reported in the literature (1.1 - 7 km/day) it seems reasonable to use them as rough estimates of the daily distances travelled by these Exmoor mares.

4.6 CONCLUSIONS

1. Ponies increase the time spent grazing and their bite rate in winter when sward height is relatively short and assumed to be of lower quality. Their speed of grazing also increases and, when considered together, these increases in activity may increase the total energy cost of grazing in the winter in comparison to the summer.

2. Ponies choose locations sheltered from the prevailing winds when inactive at all times of the year, except when ambient temperatures are high and wind speeds are less than ~5 m/s during sunny conditions in summer, and when lying on well drained areas of the field in winter. This suggests that resting sites are chosen on the basis of thermoregulation.

3. The preference of ponies to turn their hindquarters into wind is evident at all wind speeds above 1 m/s in the winter, and the same preference plus facing into the wind rather than standing sideways to it, is clear in winds of 5 m/s in the summer. This suggests that body orientation in relation to wind direction whilst grazing is a form of sheltering and may reduce their rate of heat loss.

4. The daily distances travelled (excluding grazing) by the Exmoor ponies as estimated in winter and summer appeared to be similar. The speed of walking was greater in

winter than summer, but the time spent walking was shorter in winter than in summer. Energy costs for this activity may not change significantly between seasons.

4.7 FUTURE WORK

1. The behaviour of ponies during gathering days needs to be studied in relation to the energy requirements on that day and disruption to normal feeding and resting activity.

2. The relationship between the topographical and botanical features of an area in relation to prevailing winds may be used to indicate the quality of shelter available to ponies and horses of particular sizes and would be an important management tool. However, the development of a shelter or exposure index related to these physical features requires further study.

3. Whilst horses may spend considerable periods of time in wet locations, they require dry areas to fulfill their minimal requirements for paradoxical sleep. Mapping such locations and their areas when the home range is at field capacity in relation to the stocking density of a site should be considered before horses are put on new ranges, for instance when used on sites of botanical interest. Studies of the spatial relationships between horses when lying down are also required before areas of appropriate size can be recommended.

CHAPTER 5

ESTIMATING THE DAILY ENERGY EXPENDITURE OF FREE-LIVING HORSES

This thesis includes the first reported study of measurement of the energy costs for horses of walking on different, natural ground surfaces (2.4.5). The findings have confirmed that, as for other ungulates, soft ground surfaces significantly increase the energy costs of locomotion, and that the additional cost should be included in estimations of the energy costs of locomotion. The study of the metabolic rate of Shetland ponies with wet or dry winter coats suggested that these ponies may be similar to cattle in their response to rain when ambient temperatures are around 0 °C and there is no wind (3.4.5). These findings can be used in the estimation of energy requirements of horses living outdoors, and those which are exercised or worked on natural ground surfaces. However, they must be used in conjunction with other sources of information which relate to the energy expenditure for thermoregulation and grazing in order to estimate the daily energy expenditure of M & M ponies.

5.1 Estimating energy expenditure and nutritional energy requirements

In nutritional terms, the proportion of food energy (gross energy; GE) available to the body after losses in faeces is termed digestible energy (DE), and the energy left after energy lost as urine and methane have been subtracted from DE is called metabolizable energy (ME) (McDonald et al., 1995). Further energy costs are incurred in the metabolism of ME, in the form of sugar, fatty acid and amino acid molecules, to produce available energy i.e. the high energy bond in adenosine triphosphate (ATP). The net amount of energy available to the animal, after all losses have been taken into consideration, is termed net energy (NE).

When an animal is at zero energy balance it is using all the NE produced from its food for the maintenance of body processes (NE_m) and for the metabolism of ME. The values of energy expenditure estimated from the heat equivalents of O_2 and CO_2, and the rate of respiratory exchange indicate the heat production (HP) of an animal (Blaxter, 1989). Heat production is the sum of NE_m and the heat increment (HI) of feeding i.e. the NE used during the metabolism of ME (Lawrence, 1989). Therefore, energy expenditure estimated from respiratory exchange equates to the ME expenditure of the animal.

The energy balance of the Shetland and Exmoor ponies, in which the energy costs of locomotion were measured in this thesis, was assumed to be close to zero because they were not gaining or losing significant amounts of weight (McDonald et al., 1995). Therefore, the measures of standing metabolic rate (SMR) obtained in this thesis were assumed to give an estimate of the ME required by Shetland and Exmoor ponies for maintenance when fed on hay.

The SMR of the Shetland ponies in the current study was measured under field conditions prior to exercise and, from the difference between the measured SMR of 1.37 W/kg and that estimated from the relationship between TEw and walking speed, 1.33 W/kg, anticipation of exercise may have increased SMR by ~3 %. Therefore, SMR for the Exmoor ponies was used as the basis for estimations of the ME requirements for maintenance of free-living Exmoor mares, after a deduction of 3%. This gave a figure of 1.36 W/kg which, when multiplied by a body weight of 330 kg, gave an estimated daily ME requirement for maintenance of 38.78 MJ/d.

The validity of this value was tested by comparing it to values estimated in three ways; from basal metabolic rate (BMR), calculated from general equations relating body weight to BMR in mammals (Brody, 1945; Kleiber, 1961); the BMR reported for horses by Voit (1901; cited by Blaxter,1989); and SMR measured by indirect calorimetry in two published studies (Pagan and Hintz, 1986a; Vermorel, Martin-Rosset and Vernet, 1997). All calculations were based on a liveweight of 330 kg rather than metabolic body weight ($W^{0.75}$) because Pagan and Hintz (1986a) concluded that maintenance energy expenditure of horses from 125 - 856 kg could be accurately estimated on a whole body weight basis.

The energetic efficiency (k) of converting ME to NE for maintenance (k_m) depends on the molecular form of ME, which in turn depends on the diet. Forages with a greater cellulose and lignin content have a higher HI than fresh grass, which has a higher HI than grain. The k_m values for diets decrease as HI increases, for example k_m = 61 % for poor quality hay, 65.2 % for fresh grass and 77.8 % for oats (Vermorel, Martin-Rosset, and Vernet, 1997). The values for poor hay and grass were used in the comparisons (Table 5.1) to approximate the ME values estimated from BMR to winter and summer grazing conditions.

Table 5.1; A comparison of the daily metabolisable energy requirements for maintenance (ME_m; MJ/d) of a pony (weighing 330 kg and at zero energy balance) as estimated from basal metabolic rate assuming an efficiency of utilization (k_m) of 61 % (poor hay) and 65.2 % (grass), and as estimated from indirect calorimetric measurements of standing metabolic rate (SMR) in this thesis and in two other studies.

				MJ/d		
Source	*equation*	*BMR*	*ME* *k_m 61 %*	ΔME *k_m 61 %*	*ME* *k_m 65.2 %*	ΔME *k_m 65.2 %*
Voit (1901) cited by Blaxter (1989)	3.97 MJ/d/m^2 of body surface area	23.45	38.0	+11.4%	35.97	+12.7%
Brody (1945)	$(70.5W^{0.734}) \times 0.004$	**20.82**	**34.12**	**100%**	**31.93**	**100%**
Kleiber (1961)	$(70W^{0.75}) \times 0.004$	22.68	37.17	+ 8.9%	34.79	+9.0%
	diet		*ME (SMR)*		*ME (SMR)*	
This thesis*	hay		38.78	+13.7%	38.78	+21.5%
Vermorel et al. (1997)$	forage based		37.38	+ 9.6%	37.38	+17.1%
Pagan and Hintz (1986a)#	pellets (75 % alfalfa meal + 25 % oats)		32.93	- 3.5%	32.93	+3.1%

ΔME = change in ME in relation to the lowest estimate of BMR.

* energy balance and k_m not known.

$ mean from diets with various values of k_m and horses in positive and negative energy balance.

ponies at zero energy balance, k_m not known.

The differences in ME_m between the measured values and those estimated from BMR and k_m values may have occurred for several reasons. The ponies used by Pagan and Hintz (1986a) were fed a diet which probably had a greater k_m value and lower HI than the values used in the first calculations, but a lower k_m and higher HI than those used in the second calculations in Table 5.1.

Another source of the differences may have been that the horses used by Vermorel et al. (1997) were more frequently in positive than negative energy balance, and the animals used in this thesis may also have been in positive energy balance. The k values for increasing body stores (k_f; fattening) are different to those for maintenance, and also vary with the dietary source of ME; k_f = 35 % for hay which had a k_m of 66 % (Vermorel et al., 1997). The HI of fattening is additional to that for maintenance, therefore the total energy expenditure would be greater in animals laying down fat stores.

Some of the differences in ME between calculations based on BMR, those from ponies at zero energy balance (Pagan and Hintz, 1986a) and the greatest estimates (This thesis and Vermorel et al., 1997) could have been related to another factor. The metabolic rate of an animal is known to decrease during fasting to values below those of animals fed maintenance rations and this is thought to be associated with a decrease in the metabolic rate of tissues other than, and in addition to, those of the gastro-intestinal tract (Webster, 1980). Also, animals fed on a high plane of nutrition have a greater ME_m than those accustomed to diets at or below maintenance (Hudson and Christopherson, 1985). Therefore, using BMR may underestimate the ME_m of non-fasted animals, and ME_m calculated for horses at zero energy balance (Pagan and Hintz, 1986a) may underestimate the ME_m of those in positive energy balance even when the HI of fattening has been allowed for.

Taking all these factors into consideration, the figure of 38.78 MJ/d seems a reasonable estimation of the ME_m of Exmoor ponies in winter. Depending on the quality of grass available in the summer, a value of 38.78 MJ/d may lead to overestimations of ~9 - 21 % (Table 5.1).

5.2 Estimating the daily ME requirements of free-living ponies

A factorial approach is standard in nutritional and energetic calculations (Lawrence and Stibbards, 1990, Martin-Rosset et al., 1994). An adaptation of the factorial method used by A.F.R.C. (1993) for the calculation of the daily NE requirements for maintenance and production (NE_{mp}) in domestic ruminants was used as the basis of the estimations of daily ME requirements for ponies.

For ruminants:-

$$NE_m \text{ (MJ/d)} = \text{BMR} + \text{activity allowance}$$

For ponies:-

$$ME_m \text{ (MJ/d)} = \text{SMR} + \text{production} + \text{activity}$$

5.2.1 Daily ME requirements for maintenance

Basal metabolic rate assumes that animals are lying down. Unlike ruminants, horses do not appear to have an additional energy cost for standing, above that required for lying (Winchester, 1943). Therefore, standing metabolic rate (SMR) was used in the current estimations instead of resting (lying) metabolic rate. As discussed earlier, SMR is equivalent to ME_m, assuming zero energy balance, and the calculations will be based on ME_m = 38.78 MJ/d. The energy costs of locomotion were estimated as NE (Chapter 2), therefore the different categories of activity allowance will be calculated as NE before conversion to ME by using appropriate k_m values.

5.2.1.1 Daily ME requirements for thermoregulation

The actual relationship between effective ambient temperature and the metabolic rate of horses has not been established under field conditions (Cymbaluk, 1994). Although the metabolic rates of the Shetland ponies did not vary after they were wetted, much more work needs to be completed before the influence of specific combinations of wind, temperature and precipitation can be used to estimate the rate of heat loss from acclimatised ponies. However, from the way in which ponies shelter from prevailing winds whilst both resting and grazing it would be prudent to make allowances for the energy costs of maintaining core body temperature in the winter (CRB & AAPCA, 1991). Until field measures become available, the published feed requirements of horses under mild, average and harsh winter conditions in the North East of Scotland give indications of the influence of winter weather conditions on maintenance energy requirements (CRB & AAPCA, 1991). These values will, most probably, be overestimates as the mechanical models were continuously exposed and could not "shelter" or use short-term changes in core temperature and circulation which may occur in free-living horses during short periods of colder conditions (Kaseda, 1983b). However, overestimation is preferable to underestimation when there is a danger that recommendations based on the latter values may result in underfeeding and loss of condition.

According to CRB & AAPCA (1991) the daily maintenance energy requirements of horses weighing 330 kg were estimated to increase by 29.2 % and 52.1 % during mild and harsh winters respectively. In the summer, no additional costs for thermoregulation have been estimated in horses and, as M&M ponies improve body condition (stored energy) during this season (Pollock, 1980), the influences of the climate on the rate of heat loss are not thought to be significant. However, the Exmoor mares did rest in areas sheltered from the wind at night and preferred not to graze sideways to the wind, even though the winds were light. Shelter from summer rain is thought to be critically important for smaller ungulates such as black-tailed deer (Parker, 1988) so further work may show an energy cost for ponies associated with climatic energy demand in a cool, wet summer.

Winter,

mild 0.397 W/kg harsh 0.709 W/kg

Assuming a body weight of 330 kg, these values would represent a daily ME cost of :-

mild $(0.397 \times 86400 \text{ s} \times 330 \text{ kg})/10^6 = 11.32$ MJ/d

harsh $(0.709 \times 86400 \text{ s} \times 330 \text{ kg})/10^6 = 20.20$ MJ/d

5.2.1.2 Daily ME requirements for production

Standard increases in energy requirements due to pregnancy and lactation can be added to ME_m. In the case of the Exmoors they were in the last trimester of pregnancy during the winter observation period, which indicates average costs of 115 % of ME_m (NRC, 1989), whilst the first three months of lactation can be equated to 190 % of ME_m according to the formula used by NRC (1989) for ponies of 200 kg body weight.

When ME_m = 38.78 MJ/d, the additional ME requirements for gestation would be 5.82 MJ/d, and for lactation 34.90 MJ/d.

5.2.2 Daily ME requirements for activity

The energy costs of activity, as estimated from measurements of respiratory exchange and using a factorial method, represent the NE costs. On any particular diet the efficiency of utilisation of NE for work (k_w) is the same as that for maintenance as both processes require ATP (Vermorel and Martin-Rosset, 1997). The activity allowance for cattle (section 5.2) was based on the daily distance travelled, the time spent standing and the number of position changes per day (one change = lie down plus stand up). The AFRC (1993) costs were calculated from standard values (ARC, 1980) for the additional net energy costs of standing (10 kJ/kg/d), changing posture (260 J/kg), horizontal movement (2.0 J/kg/m) and vertical movement (28 J/kg/m).

The ME activity allowance for the Exmoor mares was calculated in terms of NE, based on their 24 hour time-budgets during the winter and summer (Figures 4.4 and 4.5), and then expressed as ME, assuming k_w of 61 % in the winter and 65.2 % in the summer.

5.2.2.1 Daily NE costs of position changes

The energy costs of position changes have not been recorded for horses, but because cattle have a similar range of body weights and heights, although the manner of getting up and down is different, the energy costs for cattle have been used as an approximation. The energy costs used by AFRC (1993) for this activity, 260 J/kg, were measured in cattle weighing 460 kg (Clark, Holter, Colovos and Hayes, 1972), and are considerably greater than the costs of 104.6 J/kg measured in smaller cattle (350 kg) by Hall and Brody (1933). As the body weight of the smaller cattle is closer to the weight of the Exmoor ponies used in this thesis, the latter estimate (104.6 J/kg body weight) has been used.

Horses do get down to roll or lie down for some time during the day when it is not raining so a minimal allowance of two position changes (standing up twice and lying down twice) will be calculated.

The costs of locomotion are directly related to total body weight i.e. horse plus rider (Pagan and Hintz, 1986b), or mare plus foetus and placenta. Allowing an additional 22 kg for the average weight of the foetus and placenta during the last three months of gestation (Lewis, 1995), the NE cost of position changes could be estimated as:-

Winter $(2 \times 104.6 \text{ J/kg} \times 352)/10^6 = 0.074$ MJ/d

Summer $(2 \times 104.6 \text{ J/kg} \times 330)/10^6 = 0.069$ MJ/d

After conversion to ME using a k_w of 61 % in the winter and 65.2 % in the summer, these values become 0.12 and 0.11 MJ/d and represent an insignificant additional cost of 0.3 % of ME_m (38.78 MJ/d).

5.2.2.2 Daily NE costs of moving

The total daily distances travelled by the ponies varied according to season and according to the method of estimation (4.4.2.2). The additional costs of walking, above SMR, do not vary with speed when expressed as J/kg/m, and it was assumed that the Exmoor mares would have a similar energy cost of walking to that of the Exmoor geldings which had an average NE cost of 0.925 J/kg/m (2.3.7.2).

Allowances for a softer terrain in winter have been estimated from the difference in energy costs (Ew = 2.97 J/kg/m) between walking in mud, with a sinking depth of 12.4 cm, and walking on concrete with zero sinking depth (2.4.5).

Ew J/kg/m = 0.24 sinking depth (cm)

Assuming that the relationship between sinking depth and additional energy cost is linear, although this has not been established, and that the relationship for Exmoor ponies is similar to that in Shetland ponies may result in an overestimation for the taller Exmoors. Also, there were very few areas of the field in which the Exmoor mares sank into mud over their hooves. However, the ground under the grass mat was soft, so a conservative estimate of 1 cm has been used to calculate an allowance for the effect of ground and herbage conditions on the energy costs of locomotion in winter.

This would give a NE cost of 0.925 + 0.24 = 1.165 J/kg/m.

An energy increment due to the longer sward in summer may also be appropriate, but an allowance has not been made on the basis that the soil surface was firm in comparison to its condition in the winter, and that the ponies tended to walk longer distances on animal tracks which had little or no grass on them.

The average slope of the ground on which the ponies moved whilst grazing and walking has been estimated from the information in Appendices 4.1 and 4.7, using the equation:-

$$\text{average slope} = \frac{\Sigma_{\text{all quadrats}}\,(\text{gradient x number of scan observations})}{\text{total number of scan observations}}$$

In winter the average slopes were 7.8 % for grazing and 9.4 % for walking and, from Table 2.2, may have energy costs of 5.5 J/kg/m for uphill movement and 0.6 J/kg/m for downhill movement. In summer the slopes were 4.5 % for grazing and 5.6 % for walking, and may have energy costs of 3.27 J/kg/m for uphill, and 1.0 J/kg/m for downhill movement.

Records were not kept of the direction of movement of the ponies in relation to the slopes, therefore the principle used to estimate the orientation of ponies in relation to the wind (Figure 4.3) has been used to assume that ponies spent 25 % of the time moving directly up and down the slopes, and 50 % of the time walking across them i.e. on “level” ground. The proportions of the daily distances moved whilst grazing and walking could not be separated in the distances estimated by the quadrat method (4.3.3.6). Therefore, the proportions estimated from the time-budgets and speed of movement were used i.e. in winter, grazing = 64.5 % and walking = 35.5 % of the total daily distance, whilst in summer grazing = 21.1 % and walking = 78.9 % of the total daily distance.

Therefore, the range of distances per season and activity were estimated as:-

Winter	grazing	2014 m/d - 3583 m/d
	walking	1109 m/d - 1970 m/d
Summer	grazing	792 m/d - 1018 m/d
	walking	2958 m/d - 3810 m/d

For the Exmoor mares, the estimated energy costs of moving were based on these distances, and the estimated rates of energy expenditure. The resulting estimations of daily energy expenditure for movement are shown in Table 5.2.

Table 5.2; Estimated daily NE and ME expenditure (MJ/d) for the movements of an Exmoor pony mare (330 kg body weight) during summer (k_w = 65.2 %), and when pregnant (352 kg body weight) during winter (k_w = 61 %).

Winter

		Graze		*Walk*	
	J/kg/m	2014 m/d	3583 m/d	1109 m/d	1970 m/d
level	1.165	1170.8	2087.1	645.51	1147.5
uphill	5.5	2769.25	4926.6	1523.5	2708.75
downhill	0.6	302.1	537.5	166.2	295.5
	J/kg/d	4242.15	7551.2	2335.21	4151.75
NE	**Total MJ/d**	**1.49**	**2.66**	**0.82**	**1.46**
ME	**Total MJ/d**	**2.44**	**4.36**	**1.34**	**2.39**

Summer

		Graze		*Walk*	
	J/kg/m	792 m/d	1018 m/d	2958 m/d	3810 m/d
level	0.925	366.3	470.8	1368.08	1762.1
uphill	3.27	647.46	832.2	2418.16	3114.7
downhill	1.0	198.0	254.5	739.5	952.5
	J/kg/d	**1211.76**	**1557.5**	**4525.74**	**5829.3**
NE	**Total MJ/d**	**0.40**	**0.51**	**1.49**	**1.92**
ME	**Total MJ/d**	**0.61**	**0.78**	**2.28**	**2.94**

5.2.2.3 Daily ME costs of grazing

The energy costs of grazing *per se* have not been measured in horses. However, the energy costs of eating hay have been estimated to be 35 - 40 % of SMR in ponies (Vermorel and Mormede, 1991) and found to be comparable to the costs of 36 - 55 % of SMR for cattle and sheep (Osuji, Gordon and Webster, 1975). The energy expenditure of cattle grazing after a 24 hour fast was estimated using indirect calorimetry and found to be 52 % greater than the fasting energy expenditure, but 15 % greater than postprandial, resting energy expenditure (di Marco, Aello and Mendez, 1996). Assuming that the 15 % difference between the energy expenditure of the cattle whilst grazing and their postprandial energy expenditure indicated the proportion of the total grazing costs due to the muscular activity of selecting, biting and chewing grass, and moving, the same proportion of SMR may be appropriate for grazing activity in non-fasted ponies.

The bite rates of these cattle grazing a sward of 10.5 (s.e. 2.01) cm were 59 (s.e. 2) bites/min (di Marco, Aello and Mendez, 1996), and are similar to those of the Exmoor mares, 52 - 61 bites/min (Table 4.15). Therefore, a value of 15 % of SMR was used in the following calculation.

Based on the time spent grazing by the Exmoor mares in winter (71.5 % of 24 hours) and summer (56.1 % of 24 hours) the ME costs per day may be estimated as:-

Winter $(1.36 \text{ W/kg} \times 0.15 \times 61776 \text{ s} \times 352 \text{ kg})/10^6 = 4.44 \text{ MJ/d}$

Summer $(1.36 \text{ W/kg} \times 0.15 \times 48470 \text{ s} \times 330 \text{ kg})/10^6 = 3.26 \text{ MJ/d}$

5.3 Estimated daily ME requirement of Exmoor pony mares for maintenance, thermoregulation, production and activity.

From the summary of the results in Table 5.3, the total energy expenditure for activity may add 21.5 - 29.2 % to maintenance enegy expenditure in winter, and 16.1 - 18.3 % in summer. Grazing alone may add significantly to maintenance energy expenditure; 11.4 and 8.4 % in winter and summer respectively. Movement associated with grazing may also be a significant energy cost in winter adding a further 6.3 - 11.2 %, but not in summer when the additional costs were 1.6 - 2 %. However, the relationship between the energy expenditure for movement whilst grazing and that estimated from measurements made in horses walking steadily has not been established so these costs may not be additive. This possibly results in an overestimation, but the significance of this error can not be determined until the energy expenditure for grazing has been studied in horses.

Table 5.3; Estimated daily ME requirement (MJ/d) for maintenance, production and activity of an Exmoor pony mare in the last trimester of pregnancy (330 + 22 kg) in the winter, and during the first three months of lactation in the summer (330 kg).

		Energy expenditure (MJ/d)				
		Winter			*Summer*	
Maintenance		38.78			38.78	
weather	mild		harsh			
thermoregulation	11.32		20.20			
Production						
gestation		5.82				
lactation					34.90	
Total ME for maintenance and production	**55.92**		**64.80**		**73.68**	
Activity allowance						
position changes		0.12			0.11	
grazing		4.44			3.26	
movement	minimum		maximum	minimum		maximum
grazing	2.44		4.36	0.61		0.78
walking	1.34		2.39	2.28		2.94
Total activity allowance	**8.34**		**11.31**	**6.26**		**7.09**
Total ME requirement per day	**64.26**		**76.11**	**79.94**		**80.77**

The reasons why the energy expenditure for thermoregulation in winter may also be overestimated have been discussed earlier. However, the use by the Exmoor mares of areas sheltered from prevailing winds, and the orientation of ponies with their head or tail into the wind whilst grazing probably relates to increases in climatic energy demand (CED). Sheep reduce heat loss by 25 % when orientated with their hindquarters to the wind instead of their sides (Blaxter, 1964), therefore, the estimated requirements for thermoregulation in ponies may overestimate by approximately this amount when ponies are grazing and by a greater amount when ponies are resting in areas of reduced wind speed. However, there are other factors which may increase the dietary ME requirements of ponies, such as the health of the animal; worm burden (Gill, 1991; Burton; 1992); poor dentition (Berger, 1986); and the extra energy requirements associated with delayed weaning and poor body condition (Welsh, 1975; Tyler, 1972; Pollock, 1980).

Table 5.4; Comparison of the estimated daily ME requirements calculated in this study with those calculated according to NRC (1989), and the estimated daily ME intake of New Forest ponies.

ME (MJ/d)

Month	*ME_m*		*total daily ME*		*daily intake*[#]
	this study	NRC (1989)	this study	NRC (1989)	(Putman, 1986)
March	38.78	42.55	64.26 - 76.11	48.93	29.04
July	38.78	42.55	79.94 - 80.77	81.92	54.69

[#] estimated from gross energy figures by using a conversion factor of 35.5 % for March, based on a hay diet, and 52.4 % for the July values based on grass (Vermorel and Martin-Rosset, 1997; Vermorel et al., 1997).

The gross energy (GE) intake of New Forest ponies, as estimated from the plant composition of their faeces (Putman, 1986), was at its lowest in March, 81.8 MJ/d, and reached a peak of 139.2 MJ/d in November. The values in Table 5.4 are, therefore, part of a yearly pattern which includes periods when ME_m requirements are not met by the diet. The total daily ME requirements estimated from calculations in this study and from NRC (1989) seem to suggest that the New Forest ponies would be in negative energy balance even in mid summer. This contradicts the evidence from field-studies which have reported increases in the body condition of ponies during the summer (Pollock, 1980; Gill, 1991). It also indicates that ponies should be studied in their normal environment as those kept under less demanding conditions will not show the behavioural and physiological adaptations which may enable free-living ponies to live on marginal land.

The current method of using body condition scores as a means of establishing the fitness of individual ponies, and their population as a whole, appears to be the most practical method available when used in conjunction with local knowledge of the carrying capacity of the area. However, a greater understanding of the energy requirements of these ponies, and their interaction with their environment may be gained in the future from the application of modern tracking methods (global positioning systems, Booth, Pearson and Cuddeford, 1995) and nutritional techniques (alkane analysis, Dove and Mayes, 1991) both of which would have minimal impact on the behaviour of the animals studied.

5.4 Future Work

1. Future estimations of the energy requirements of free-living ponies need to consider seasonal variation in the nutritional environment of the animals, their daily time budgets and climatic energy demand. It may be that use of a combination of indirect calorimetric techniques in the field, such as long-term carbon dioxide dilution, doubly-labelled water (Blaxter, 1989) and short term respiratory exchange in tracheostomized, grazing animals (Wickstrom, Robbins, Hanley, Spalinger and Parish, 1984) may give more reliable estimations of daily and seasonal energy expenditure than the application of laboratory measurements.

2. Alkane analysis has proven to be a very useful technique in identifying the dietary components of both wild and domestic herbivores and in estimating intake (Dove and Mayes, 1991). This technique would enable more accurate estimations of the energy content and intake of the diet of free-living horses and ponies and would complement studies of energetics and behaviour.

3. Many domestic horses also spend time outdoors, and the application of such techniques to these situations also has the potential to increase knowledge of the influence of a wide range of management practices on the energy expenditure and the contribution of grazing to food intake in horses living and working outdoors, thereby improving their welfare.

4. The net energy costs of thermoregulation and grazing are currently not well understood in horses and, because of their implications for welfare and the formulation of diets, they require detailed investigation in both free-living and pastured, domestic horses.

5. The influence of natural ground surfaces on the energy costs of locomotion in all types of horses needs further investigation, and has implications for sport horses, agricultural draught and pack-horses as well as free-living horses. The field investigations made during this study have shown that the Oxylog is a reliable tool for such studies and its application could add valuable information in this area of research.

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Appendix 2.1

The normal walking speed (m/s) of four Shetland ponies (Animals 1-4) and three Exmoor ponies (Animals 5-7) on outward and homeward journeys

Shetland No.	*Speed “out” m/s*	*Speed “home” m/s*	*Exmoor No.*	*Speed “out m/s*	*Speed “home” m/s*
1	1.242	1.293	5	1.073	1.102
1	1.134	1.096	5	1.071	1.089
1	1.144	1.157	5	0978	1.077
1	1.162	1.264	5	0928	1.035
2	0.973	1.030	6	1.179	1.278
2	1.022	1.143	6	1.195	1.303
2	1.067	1.029	6	1.188	1.234
2	1.026	1.054	6	1.196	1.185
3	1.083	1.135	7	1.207	1.286
3	1.095	1.218	7	1.145	1.324
3	1.130	1.075	7	1.239	1.313
3	1.091	1.040	7	1.230	1.358
4	1.099	1.087			
4	1.153	1.186			
4	1.065	1.113			
4	1.021	1.060			

Data analysis:-

The mean data (speed) were subjected to an analysis of variance (SAS, 1985) as the measurements were taken in succession. "Animal" was used as the error term to test the effect of journey type on the speed of walking (Appendix 2.2).

Results:-

There were no significant differences between breeds in speed of walking (*P*=0.539), but the speeds of the different journeys, "out" or "home", were significantly different (*P*<0.001; see Table below).

Appendix 2.1/cont.

The mean s.e. speed (m/s) of seven different ponies, four Shetland and three Exmoor, walking on four outward and four homeward journeys, and the mean s.e. walking speed of each breed group.

Breed	*Animal*	*walking speed (m/s)*			
		mean (s.e.)			
		out (n=4)	*home (n=4)*	*Breed*	*Significance*
Shetland	1	**1.16 (0.025)**	**1.19 (0.045)**	**1.11 (0.012)** **(n=32)**	**NS**
	2	**1.01 (0.018)**	**1.05 (0.026)**		
	3	**1.10 (0.009)**	**1.12 (0.038)**		
	4	**1.07 (0.028)**	**1.10 (0.026)**		
Exmoor	5	**1.00 (0.036)**	**1.08 (0.015)**	**1.18 (0.023)** **(n=24)**	
	6	**1.19 (0.003)**	**1.24 (0.025)**		
	7	**1.21 (0.020)**	**1.31 (0.014)**		
Significance			***		

*** indicates significant differences *P*<0.001 NS = not significantly different *P*>0.05

Appendix 2.2

Analysis of variance of walking speed in Shetland and Exmoor ponies based on the mean for each animal for each journey, "out" and "home".

SAS (1985) General Linear Models Procedure

Tests of hypotheses for Random Model Analysis of Variance

Dependent variable: speed (m/s)

Model: $y_{ijkl} = A_i + B_{ij} + D_{ijk} + E_{ijkl}$

i = breed (1,2) j = pony (1-7) k = journey (1,2) l = error

Source : Breed

Error: MS(Pony(Breed))

DF	Type III MS	Denominator DF	Denominator MS	F	Pr>F
1	0.0118453125	5	0.0272554375	0.4346	0.5389

Source: Pony(Breed)

Error: MS(Pony(Breed))

DF	Type III MS	Denominator DF	Denominator MS	F	Pr>F
1	0.0272554375	21	0.0020596905	13.2328	0.0001

Appendix 2.3

Stride length (m) and stride frequency (strides/min) of four Shetland ponies walking on a level treadmill at four different speeds during random allocation of speed (Period 1) and sequential allocation of speed (1-4; Period 2).

		Period 1		*Period 2*	
Speed (m/s)	**Animal**	**stride length (m)**	**stride frequency (strides/min)**	**stride length (m)**	**stride frequency (strides/min)**
1 (0.34)	**1**	*	*	**0.64**	**30.5**
	2	*	*	**0.63**	**34.8**
	3	*	*	**0.67**	**32.7**
	4	*	*	**0.72**	**29.4**
2 (0.63)	**1**	**1.00**	**37.6**	**0.77**	**47.9**
	2	**1.04**	**37.0**	**0.74**	**51.6**
	3	**0.95**	**40.6**	**0.87**	**43.0**
	4	**0.88**	**42.3**	**0.9**	**41.0**
3 (0.87)	**1**	**0.86**	**61.4**	**0.88**	**58.4**
	2	**0.90**	**59.1**	**0.87**	**60.3**
	3	**0.82**	**62.8**	**1.00**	**52.2**
	4	**0.77**	**66.3**	**0.96**	**52.6**
4 (1.12)	**1**	**0.76**	**92.0**	**1.03**	**64.7**
	2	**0.78**	**88.1**	**1.00**	**67.4**
	3	**0.73**	**93.8**	**1.08**	**62.4**
	4	**0.71**	**97.2**	**1.09**	**59.9**

Appendix 2.4

The gross energy requirements of Shetland ponies (Animals 1-4) for standing (SMR), and their gross (TEw) and net (Ew) energy requirements for walking at four different speeds on a level treadmill.

Animal	*Speed 1 (m/s)*	*SMR (W/kg)*	*TEw (W/kg)*	*Ew (J/kg/m)*
1	0.336	1.425	1.831	1.212
1	0.246	1.621	1.914	1.191
1	0.342	1.352	1.676	0.952
1	0.341	1.256	1.614	1.053
1	0.343	1.350	1.619	0.786
1	0.360	1.494	1.845	0.974
2	0.375	1.257	1.681	1.134
2	0.358	1.524	1.968	1.244
2	0.369	1.358	1.768	1.114
2	0.343	1.384	1.742	1.047
2	0.369	1.504	1.914	1.116
2	0.364	1.402	1.807	1.114
3	0.377	1.566	1.924	1.025
3	0.362	1.381	1.664	0.785
3	0.361	1.510	1.893	1.060
3	0.344	1.059	1.377	0.926
3	0.355	1.475	1.769	0.828
3	0.353	1.500	1.784	0.808
4	0.339	0.986	1.472	1.433
4	0.374	1.143	1.566	1.135
4	0.373	0.940	1.324	1.031
4	0.341	0.912	1.236	0.950
4	0.343	1.000	1.374	1.092
4	0.353	1.111	1.441	0.936

Appendix 2.4 cont/.

Animal	*Speed 2 (m/s)*	*SMR (W/kg)*	*TEw (W/kg)*	*Ew (J/kg/m)*
1	0.639	1.267	2.017	1.176
1	0.632	1.494	2.123	0.995
1	0.610	1.789	2.456	1.093
1	0.632	1.551	2.277	1.151
1	0.593	1.631	2.294	0.949
1	0.622	1.670	2.270	0.965
2	0.624	1.667	2.284	0.991
2	0.659	1.532	2.292	1.155
2	0.638	1.694	2.369	1.060
2	0.649	1.708	2.578	1.340
2	0.626	1.371	2.037	1.066
2	0.643	1.472	2.168	1.082
3	0.636	1.548	2.244	1.094
3	0.640	1.364	1.937	0.897
3	0.658	1.522	2.138	0.937
3	0.617	1.435	2.015	0.940
3	0.628	1.414	1.916	0.801
3	0.638	1.431	1.962	0.837
4	0.618	1.122	1.818	1.126
4	0.605	1.083	1.821	1.222
4	0.630	1.077	1.789	1.132
4	0.615	1.238	1.933	1.132
4	0.627	1.044	1.669	0.999
4	0.564	1.148	1.706	0.989

Appendix 2.4 cont./

Animal	*Speed 3 (m/s)*	*SMR (W/kg)*	*TEw (W/kg)*	*Ew (J/kg/m)*
1	0.858	1.581	2.465	1.031
1	0.887	1.381	2.274	1.008
1	0.900	1.305	2.093	0.877
1	0.892	1.024	1.787	0.855
1	0.850	1.678	2.444	0.901
1	0.837	1.902	2.777	1.047
2	0.825	1.389	2.418	1.247
2	0.929	1.628	2.665	1.116
2	0.904	1.256	2.266	1.117
2	0.885	1.109	1.920	0.961
2	0.888	1.625	2.292	0.763
2	0.854	1.574	2.409	0.979
3	0.862	1.364	2.162	0.927
3	0.848	1.687	2.450	0.901
3	0.864	1.390	2.224	0.965
3	0.878	1.203	1.911	0.806
3	0.854	1.491	2.202	0.834
3	0.878	1.485	2.216	0.834
4	0.872	1.051	1.985	1.071
4	0.805	1.025	1.915	1.106
4	0.886	1.103	2.063	1.084
4	0.845	0.732	1.404	0.797
4	0.857	1.203	2.090	1.035
4	0.820	1.115	1.936	1.003

Appendix 2.4 cont/.

Animal	*Speed 4 (m/s)*	*SMR (W/kg)*	*TEw (W/kg)*	*Ew (J/kg/m)*
1	1.180	1.362	2.712	1.145
1	1.169	1.276	2.702	1.221
1	1.136	1.305	2.562	1.107
1	1.159	1.461	2.546	0.931
1	1.105	1.904	2.724	0.742
1	1.069	1.585	2.385	0.748
2	1.149	1.228	2.608	1.202
2	1.146	1.400	3.035	1.428
2	1.156	1.532	2.988	1.260
2	1.158	1.313	2.250	0.809
2	1.098	1.832	2.899	0.973
2	1.104	1.710	2.823	1.008
3	1.075	1.216	2.337	1.044
3	1.161	1.269	2.451	1.019
3	1.192	1.400	2.728	1.115
3	1.170	1.303	2.328	0.876
3	1.078	1.688	2.573	0.822
3	1.118	1.683	2.528	0.757
4	1.145	0.929	2.303	1.200
4	1.146	1.077	2.454	1.203
4	1.150	1.038	2.335	1.129
4	1.138	1.060	2.541	1.246
4	1.047	1.030	2.057	0.982
4	1.083	1.324	2.498	1.085

Appendix 2.5

General linear models analysis of variance for the data in Appendix 2.4 of the gross energy costs of standing (SMR, W/kg) and walking (TEw, W/kg) and the net energy cost of walking (J/kg/s) on a level treadmill at four different speeds (m/s) as measured from four different Shetland ponies.

SMR (W/kg)

Source	DF	SS	MS	F	P
Animal	3	2.969864	0.98955	32.0	0.000
Speed	3	0.17026	0.05675	1.84	0.147
Interaction	9	0.04485	0.00498	0.16	0.997
Error	80	2.47380	0.03092		
Total	95	5.65755			

TEw (W/kg)

Source	DF	SS	MS	F	P
Animal	3	2.61075	0.87025	23.51	0.000
Speed	3	9.44614	3.14871	85.08	0.000
Interaction	9	0.16646	0.01850	0.50	0.871
Error	80	2.96073	0.03701		
Total	95	15.18409			

Ew (J/kg/m)

Source	DF	SS	MS	F	P
Animal	3	0.54801	0.18267	9.93	0.000
Speed	3	0.09942	0.03314	1.80	0.154
Interaction	9	0.03470	0.00386	0.21	0.992
Error	80	1.47142	0.01839		
Total	95	2.15355			

Appendix 2.6

The gross energy requirements of Exmoor ponies (Animals 5&6) for standing (SMR), and their gross (TEw) and net (Ew) energy requirements for walking on a level, circular concrete path.

Animal	*Speed (m/s)*	*SMR (W/kg)*	*TEw (W/kg)*	*Ew (J/kg/m)*
5	0.861	1.478	2.147	0.776
5	0.823	1.715	2.375	0.809
5	0.821	1.224	1.972	0.913
5	0.797	1.348	1.892	0.678
5	0.924	0.964	1.565	0.650
5	0.871	1.601	2.228	0.721
6	0.953	1.558	2.994	1.506
6	0.979	1.466	2.604	1.164
6	0.901	1.425	2.602	1.305
6	0.904	1.355	2.119	0.843
6	0.909	1.103	1.916	0.892
6	0.967	1.626	2.589	0.993

Appendix 2.7

Measurement of the effect of carrying the Oxylog equipment on the energy costs of walking on a treadmill in Shetland ponies.

Three Shetland ponies (No. 1, 2 and 3) walked on a level treadmill at normal walking speed (~1 m/s) whilst unladen or carrying weights equivalent to the Oxylog and its wooden mask in a backpack and around the flow-through face mask. Six measurements (see Experiment 2.1 for method) of SMR and TEw, both laden and unladen, were taken from each animal from which Ew was calculated.

The total energy requirements for standing (SMR) and the net energy requirements for walking (Ew) of Shetland ponies carrying, or not, weights equivalent to the Oxylog and the wooden face-mask (8 kg in total) whilst walking on a level treadmill.

Animal	*SMR (W/kg) carrying weights*	*SMR (W/kg) without weights*	*Ew (J/kg/m) carrying weights*	*Ew (J/kg/m) without weights*
1	1.44	1.37	1.27	1.25
1	1.34	1.27	1.18	1.20
1	1.20	1.18	1.21	1.12
1	1.20	1.21	1.19	1.14
1	1.20	1.19	1.22	1.27
1	1.16	1.15	1.15	1.25
2	1.38	1.28	1.28	1.17
2	1.22	1.16	1.16	1.12
2	1.30	1.22	1.22	1.43
2	1.28	1.22	1.22	1.21
2	1.12	1.11	1.12	1.31
2	1.13	1.17	1.17	1.20
3	1.39	1.42	1.47	1.14
3	1.32	1.35	1.40	1.11
3	1.44	1.33	1.33	1.10
3	1.35	1.39	1.39	1.05
3	1.21	1.23	1.23	1.05
3	1.32	1.37	1.37	1.01

Appendix 2.7 cont/

Stride parameters (mean s.e.) under the same conditions.

Animal	*Measurements*	*Stride length (m)* *Mean (s.e.)*		*Stride frequency (strides/min)* *Mean (s.e.)*	
		with weights	**no weights**	**with weights**	**no weights**
1	**12**	**0.99 (0.012)**	**1.00 (0.018)**	**63.6 (0.29)**	**63.5 (0.22)**
2	**12**	**0.93 (0.016)**	**0.93 (0.018)**	**67.4 (0.67)**	**67.1 (0.13)**
3	**12**	**1.08 (0.012)**	**0.99 (0.010)**	**60.2 (0.90)**	**58.8 (0.54)**

STATISTICAL ANALYSIS

As measurements of energy expenditure both with and without the weights were made during the same session, the data were analysed using a paired t-test.

RESULTS

The differences in Ew between carrying and not carrying weights equivalent to the Oxylog equipment were not significant (n = 18, T = 1.94, $P = 0.069$). Neither were there any significant differences in SMR (n = 18, T = 1.72, $P = 0.1$), stride length (n=36, T = 1.82, $P = 0.077$), or stride frequency (n = 36, T = 1.89, $P = 0.066$). The mean s.e. walking speed was 0.96 (0.005) m/s.

Appendix 2.8

The net energy requirements (Ew; J/kg/m) of Shetland ponies walking on different, level ground surfaces.

Animal	*Grass*	*Concrete*	*Mud*
1	2.55	3.15	6.30
1	1.92	2.91	7.05
1	1.46	4.50	7.35
1	1.64	4.78	5.87
1	2.12	3.06	7.07
1	2.18	2.57	6.67
2	1.61	2.30	7.58
2	1.77	2.91	7.17
2	1.52	4.25	6.09
2	1.68	3.25	7.19
2	1.62	2.80	6.80
2	1.50	2.26	*
3	1.45	3.58	4.54
3	2.40	2.19	3.32
3	1.43	2.68	4.90
3	0.97	4.72	4.87
3	1.81	2.45	5.38
3	1.61	1.66	*
8	1.41	3.04	6.24
8	1.84	2.33	6.00
8	2.23	2.68	4.66
8	2.15	3.69	5.84
8	1.61	2.39	7.27
8	1.8	2.10	5.37
9	1.48	2.67	5.17
9	1.24	2.63	4.22
9	1.45	2.33	5.16
9	1.22	2.30	4.71
9	1.74	1.92	5.19
9	1.66	2.13	5.93

* = missing data

Appendix 2.9

The net energy requirements (Ew; J/kg/m) of Shetland ponies walking up and down a hill with a gradient of 5.8°, expressed as $Ew_{surface}$; per distance travelled (m) on the ground, and as $Ew_{vertical}$; per vertical height (m) ascended/descended.

Animal	$Ew_{surface}$ *up*	$Ew_{surface}$ *down*	$Ew_{vertical}$ *up*	$Ew_{vertical}$ *down*
1	8.22	5.10	35.52	12.84
1	6.15	2.50	19.11	-12.74
1	9.02	5.96	53.18	23.16
1	6.77	2.68	-17.84	-47.33
2	4.34	2.59	19.67	5.95
2	4.98	3.50	33.03	19.14
2	4.74	3.84	25.98	18.95
2	5.61	3.03	7.26	-14.47
2	4.02	2.79	6.78	-5.18
8	6.24	2.65	32.77	-1.15
8	5.12	3.53	14.59	1.02
8	5.86	4.48	26.86	16.92
8	4.94	2.74	9.96	-7.50
8	5.49	3.12	16.28	-4.16
9	4.25	2.85	1.54	-9.37
9	1.78	3.73	17.55	9.21
9	4.74	2.82	5.92	-10.68
9	4.97	2.57	23.86	4.95
9	4.00	1.64	17.45	-2.85

Appendix 2.10 The mean heart rate (bpm) of five Shetland ponies whilst standing or walking on grass, concrete, mud, up hill or down hill.

	Grass		*Concrete*		*Mud*		*Hill*		
Animal	stand	walk	stand	walk	stand	walk	stand	up	down
1	55.5	77.0	56.5	85.8	54.9	104.0	48.0	101.03	77.81
1	53.0	73.8.	59.7	77.7	49.0	92.0	52.0	95.03	90.6
1	54.2	78.6	68.9	93.0	52.0	105.0	48.1	94.72	90.95
1	62.0	79.3	66.7	91.7	49.0	85.0	53.97	106.00	87.81
1	*	*	58.0	72.9	58.0	107.0	-	-	-
1	50.9	76.0	56.3	73.9	52.0	91.0	-	-	-
2	51.2	70.8	59.3	75.6	55.0	107.0	54.13	103.45	92.86
2	53.8	74.2	58.7	71.6	59.0	108.0	44.43	97.67	83.38
2	*	*	69.6	96.2	50.0	109.0	47.46	108.91	86.81
2	*	*	60.8	87.3	52.0	106.0	46.71	106.82	86.41
2	48.5	61.7	66.05	91.8	46.0	94.0	-	-	-
2	50.2	67.0	57.2	77.7	*	*	-	-	-
3	49.0	69.2	56.8	75.2	48.0	87.0	-	-	-
3	49.6	77.2	52.55	69.0	57.0	113.0	-	-	-
3	55.0	73.8	57.35	78.1	42.0	84.0	-	-	-
3	*	*	65.5	92.44	48.0	87.0	-	-	-
3	*	*	52.35	72.3	44.0	85.0	-	-	-
3	44.2	67.5	52.1	67.9	*	*	-	-	-
8	48.3	71.0	45.0	70.3	46.0	106.0	44.54	116.03	97.11
8	54.3	83.3	45.45	64.6	47.0	101.0	52.29	113.94	98.44
8	49.3	84.0	39.7	64.8	42.0	97.0	44.82	110.16	89.10
8	49.5	75.2	47.65	79.4	41.0	107.0	51.18	118.17	99.11
8	45.6	68.8	41.85	68.0	38.0	94.0	54.10	114.41	95.66
8	49.3	78.5	40.7	64.6	40.0	85.0	-	-	-
9	51.5	74.5	48.3	71.3	70.0	104.0	57.67	114.22	89.14
9	51.7	70.5	51.65	72.9	70.0	100.0	50.50	96.6	85.25
9	49.2	70.0	51.1	67.3	58.0	110.0	50.30	102.56	80.13
9	*	*	52.6	68.8	58.0	110.0	47.78	102.56	82.33
9	49.0	66.0	52.2	70.7	59.0	105.0	52.46	107.14	83.76
9	51.3	73.2.	53.9	73.8	53.0	96.0	-	-	-

Appendix 3.1; METHOD FOR THE CARDING OF HAIR SAMPLES.

The purpose of carding is to arrange a representative sample of the coat fibres in order of length so that measurements can be taken.

Materials:-
Light-weight card of contrasting colour to the hair.
Clear adhesive tape.
A flat-ended spatula or ruler.
Scissors.

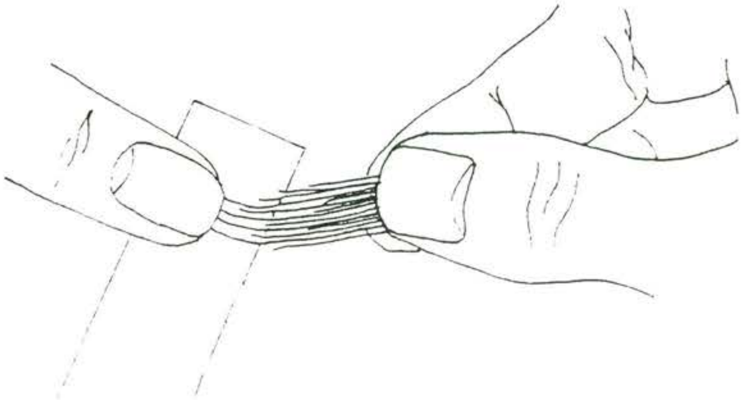
Method:-

1. Secure 25 cm of tape, adhesive side up, in the centre of the card.
2. The hair sample should be prepared by bringing the cut ends, which will be lying in a swathe, to the same level by tapping them with a finger in the direction of their tips.
3. Take a pinch sample at the levelled, cut ends using thumb and index finger. Don't let go.
4. Clear away all loose hairs using the free hand.
5. Transfer the sample to the free hand, gripping with thumb and index finger so that the hair-tips point towards the palm of that hand and the cut ends are exposed.
6. Clear away loose hairs from the cut ends.
7. If further levelling is needed, hold the sample vertically, cut ends uppermost, relax the grip slightly and tap the cut ends level with a finger.
8. Tighten the grip and pull out any hairs which still protrude more than 1 mm beyond the level cut ends.
9. Transfer the sample to the first hand, gripping close to the cut ends so that the tips protrude. Check again for loose hairs.
10. Starting at one end of the adhesive tape, place the sample so that the tips of the longest hairs are at right angles to, and touching the tape (see Figure A3.1).
11. Secure these tips, about 1 mm from their free end, with a finger or a flat ended instrument, then pull the rest of the sample away.
12. Repeat steps 10 & 11 working evenly along the tape until all hairs have been secured to the adhesive tape.

13. Some short hairs, too short to secure against the tape using step 12, may remain stuck to finger and thumb. In this case gently open finger and thumb and place them directly on the tape surface. In this way the hairs will transfer to the tape thus completing the carding of the sample.

14. To facilitate filing, and to permanently secure the sample, the sticky surface of the tape can be covered with tape, adhesive side down.

Figure A3.1; **Method for transfering hair to adhesive tape.**



Appendix 3.2; LENGTH (cm) AND DEPTH (cm) OF THE WINTER COAT OF TWO SHETLAND PONIES, FROM DIFFERENT REGIONS OF THE BODY.

	Length (cm)		Depth (cm)	
Pony	Pony 1	Pony 3	Pony 1	Pony 3
Sampling Region				
Head				
1. Masseteric region	2.2	2.0	0.5	0.5
1a.Dorsal nasal region	2.0	1.5	1.5	0.5
Neck				
2. Dorsal cervical region	5.5	4.0	4.0	3.5
3. Ventral cervical region	5.5	3.5	4.0	3.5
Thorax				
4. Interscapular region	4.0	4.0	3.0	2.5
5. Back	3.5	3.0	2.75	2.0
6. Costal region	4.0	4.5	3.5	2.75
7. Presternal region	5.0	3.5	4.5	2.5
8. Sternal region	4.0	-	4.0	-
Abdomen				
9. Xiphoid region	5.0	4.0	3.0	4.0
11. Lumbar region	4.0	3.25	2.0	1.5
12. Lateral Abdominal region	4.0	3.5	3.0	2.5
17. Tail (root of)	4.0	3.5	2.0	2.0
Forelimb				
18. Scapular region	5.0	3.5	3.0	3.0
19. Brachial region	4.5	4.0	3.5	3.5
22. Antebrachial region (lateral)	3.5	4.5*	2.0	2.0
22a Antebrachial region (medial)	5.5	3.0	1.75	1.5
23. Carpal region (dorsal)	4.0	2.0	1.0	1.0
23a Carpal region (palmar)	6.5	3.0	1.75	0.5
24. Metacarpal region (dorsal)	3.5	2.5	0.5	0.5
24a Metacarpal region (palmar)	9.5	10.5	1.0	1.5
25. Digit (dorsal)	4.0	3.0	0.5	1.5

Appendix 3.2; cont.

	Length (cm)		Depth (cm)	
Pony	Pony 1	Pony 3	Pony 1	Pony 3
Sampling Region				
Pelvis/Hindlimb				
26. Sacral region	4.5	3.5	2.0	2.0
28. Gluteal region	3.5	4.0	3.5	3.0
A Semitendinosus region	6.0	3.0*	2.5	1.5
B Semimembranosus region	1.5	1.5	0.2	0.2
31. Femoral region	3.0	3.25*	2.0	2.5
32. Region of knee (lateral)	3.0	3.5	1.5	3.25
32a Region of knee (medial)	3.5	2.0	1.0	1.5
33. Crural region (lateral)	4.0	3.5	2.0	2.0
33a Crural region (medial)	4.0	3.0	2.0	1.0
34. Tarsal region (dorsal)	3.0	2.5	1.5	1.0
34a Tarsal region (plantar)	3.5	2.5	1.5	0.5
35. Metatarsal region (dorsal)	3.0	3.0	0.5	0.5
35a Metatarsal region (plantar)	9.5	4.0	2.5	2.5
36. Digit (dorsal)	2.5	2.5	0.5	1.0

		Pony 1	Pony 3
Tail	length	93	92
	width at hocks	21.5	18
Mane	length (maximum)	64	61
Forelock	length (maximum)	34	30
	width at eyes	19	15
Fetlocks**:-	fore	9	6
	hind	6	5.5

* cat hairs present

** long hairs on the fetlocks were seasonal, not permanent hairs.

Appendix 3.3; LENGTH (cm) AND DEPTH (cm) OF THE SUMMER COAT OF A SHETLAND PONY, FROM DIFFERENT REGIONS OF THE BODY.

	Length (cm)	Depth (cm)
Pony 1		
Sampling Region		
Head		
1. Masseteric region	1.8*	0.4
1a.Dorsal nasal region	1.2	0.7
Neck		
2. Dorsal cervical region	1.2	0.8
3. Ventral cervical region	1.0*	0.8
Thorax		
4. Interscapular region	2.5	0.7
5. Back	0.9	1.0
6. Costal region	1.3	1.3
7. Presternal region	0.7	0.5
8. Sternal region	0.2	0.6
Abdomen		
9. Xiphoid region	0.8	2.0 (hanging straight down)
11. Lumbar region	0.9	0.5
12. Lateral Abdominal region	0.8	0.7
Forelimb		
18. Scapular region	1.0	0.4
19. Brachial region	0.9	0.4
22. Antebrachial region (lateral)	0.9	0.3
22a Antebrachial region (medial)	0.3	0.6
23. Carpal region (dorsal)	1.4	0.5 (dense hair, coarse)
23a Carpal region (palmar)	1.0	0.5 (finer hair)
24. Metacarpal region (dorsal)	1.0	0.4
24a Metacarpal region (palmar)	1.2	0.5
25. Digit (dorsal)	1.5	0.3

Appendix 3.3; cont.

	Length (cm)	Depth (cm)
Pony 1		
Sampling Region		
Pelvis/Hindlimb		
26. Sacral region	1.0	0.8
28. Gluteal region	1.5	0.9
17. Tail (root of)	1.75	0.8
A Semitendinosus region	0.7	0.2
B Semimembranosus region	0.7	0.5
31. Femoral region	0.8	0.5
32. Region of knee (lateral)	0.6	0.5
32a Region of knee (medial)	0.4	0.7
33. Crural region (lateral)	1.4	0.7
33a Crural region (medial)	0.3	0.6
34. Tarsal region (dorsal)	0.8	0.2
34a Tarsal region (plantar)	1.4	0.6
35. Metatarsal region (dorsal)	0.7	0.4
35a Metatarsal region (plantar)	1.5	1.0
36. Digit (dorsal)	1.5	0.7

* cat hairs present

Appendix 3.4a; **DENSITY (mg/cm²) OF THE WINTER AND SUMMER COATS OVER THE DORSAL CERVICAL, BACK AND COSTAL REGIONS OF FIVE SHETLAND PONIES.**

	Coat density (mg/cm²)			
Body region	Dorsal cervical	Back		Costal
Season	winter	winter	summer	winter
Pony No. 1	78.0	85.3	35.5	56.2
No. 2	88.9	100.8	26.7	70.0
No. 3	74.1	73.2	31.0	64.3
No. 8	65.8	120.5	27.8	115.7
No. 9	66.7	101.2	26.7	70.2

Appendix 3.4b; **DENSITY (fibres/cm²) OF THE WINTER AND SUMMER COATS OVER THE BACK OF FOUR SHETLAND PONIES.**

SEASON	*WINTER*	*SUMMER*
Pony No. 1	1032.7	914.8
No. 3	1013.8	1313.6
No. 8	1083.5	712.7
No. 9	980.5	758.4

Appendix 3.5; **MAXIMUM AND MINIMUM FIBRE LENGTHS* (mm) FROM THE WINTER COAT OVER THE DORSAL CERVICAL, BACK AND COSTAL REGIONS OF FIVE SHETLAND PONIES.**

	Fibre length (mm)					
Body region	Dorsal cervical		Back		Costal	
length	min.	max.	min.	max.	min.	max.
Pony No.1	10	90	12	50	9	58
No.2	30	59	12	51	12	49
No.3	9	61	11	49	11	84
No.8	7	59	18	92	8	97
No.9	11	47	13	48	8	87

* length includes 2 mm of coat left on the pony.

Appendix 3.6; MAXIMUM AND MINIMUM FIBRE LENGTHS* (mm) FROM THE SUMMER COAT OVER THE BACK REGION OF SIX SHETLAND PONIES.

	Fibre length (mm)	
	minimum	maximum
Pony No. 1	9	14
No. 2	6	18
No. 3	7	21
No. 4	7	22
No. 8	6	14
No. 9	5	14

* length includes 2 mm of coat left on the pony

28 **3;** 2, 3, 6, 12, 18, A, 19, 22, 31, 32, 33 **4;** 7, 8, 9, 13, 16, 22a, 32a, 33a

Appendix 3.7; CALIBRATION OF TEMPERATURE SENSORS USED IN EXPERIMENT 3.2

The Digital thermometer was calibrated using the water bath and temperature sensor of a bomb calorimeter (Parr 1261; Figure A3.2). The resulting correction calculation was:-

$$WT(^{o}C) = -0.0657 + (1.02\ \{\text{digital reading}\}) \qquad (r^2 = 100\ \%)$$

The Rectal thermometer was calibrated in the same way as the digital thermometer (Figure A3.3). The resulting correction calculation was:-

$$RT\ (^{o}C) = -1.22 + (1.02\ \{\text{rectal reading}\}) \qquad (r^2 = 100\ \%)$$

The Touch thermometer was calibrated using the water bath and two reference thermometers; the temperature sensor of a bomb calorimeter (Parr 1261) and the digital thermometer described earlier. Temperature was calculated using the following formula derived from a regression of lnR (natural log of resistance) against the reciprocal of temperature (degrees Kelvin) (Figure A3.4):-

$$\ln R = -0.0864 + 2995(1/T^{o}K) \qquad (r^2 = 100\ \%)$$

therefore:-

$$T^{o}C = (2995/\{\ln R - [-0.0864]\}) - 273.16$$

Figure A3.2; **The relationship between Reference temperature and Digital Thermometer temperature.**

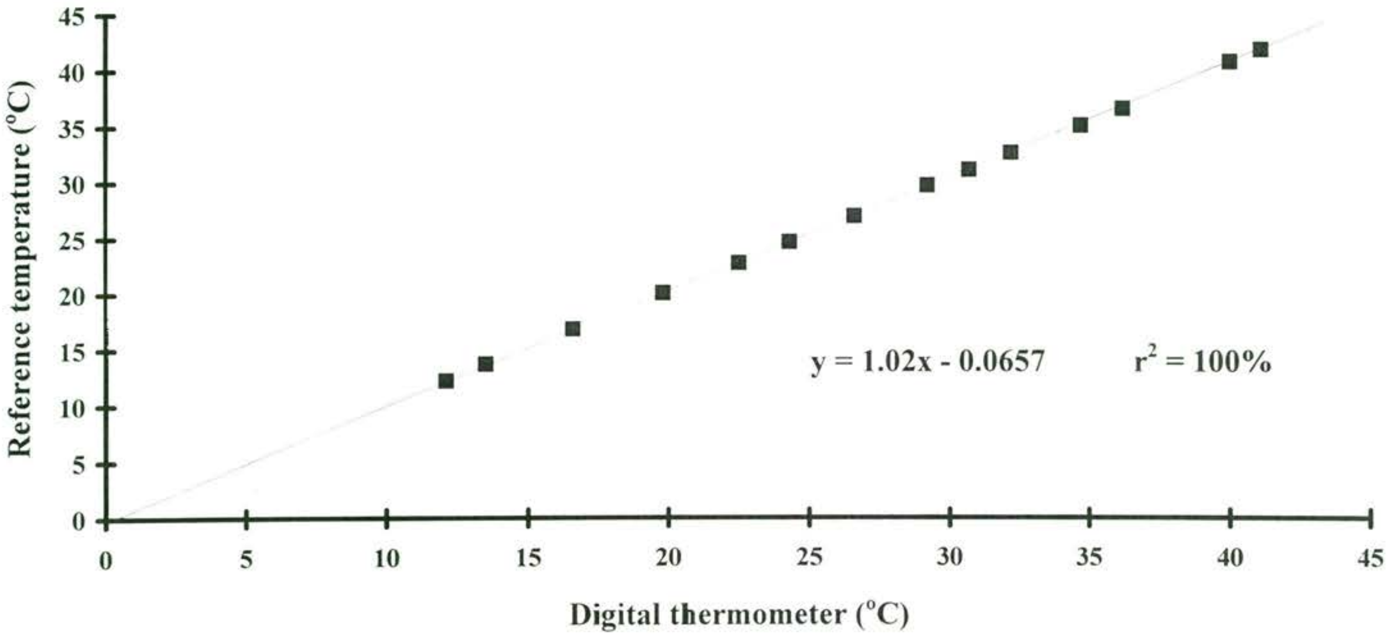


__Figure A3.3:__ **The relationship between Reference temperature and Rectal Thermometer temperature.**

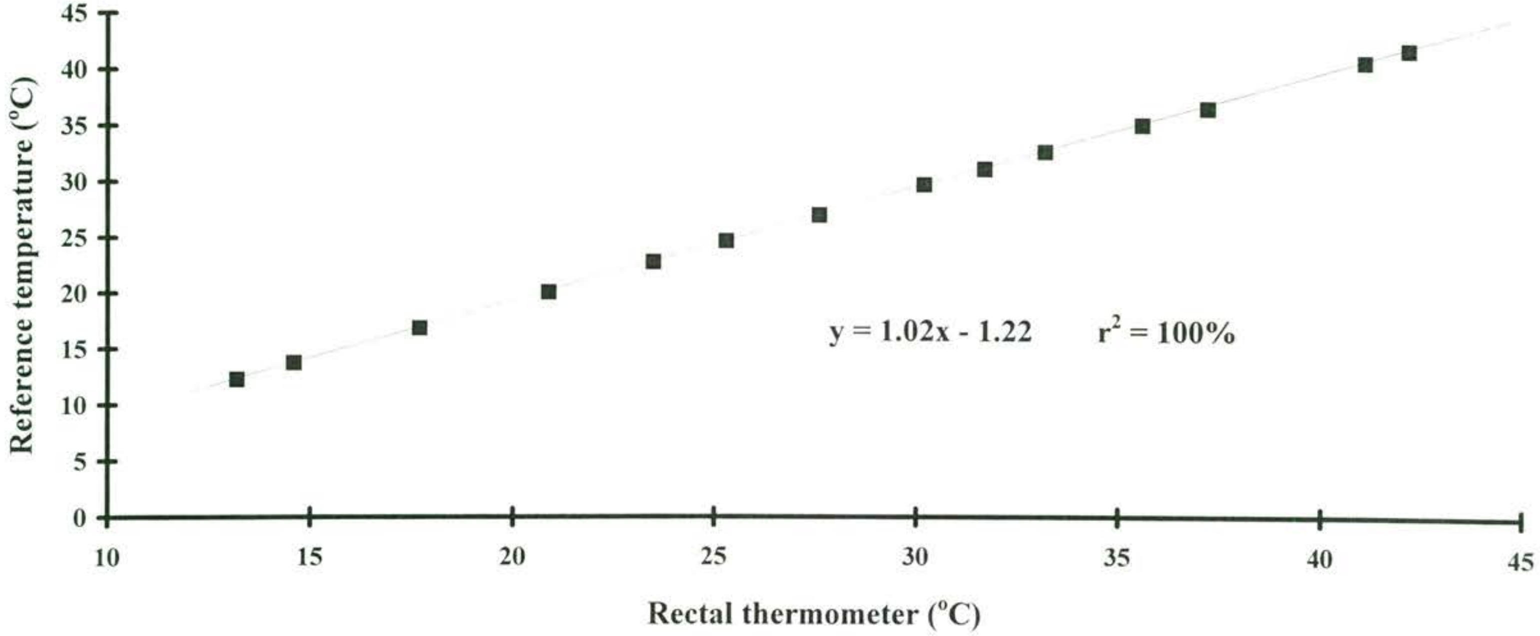
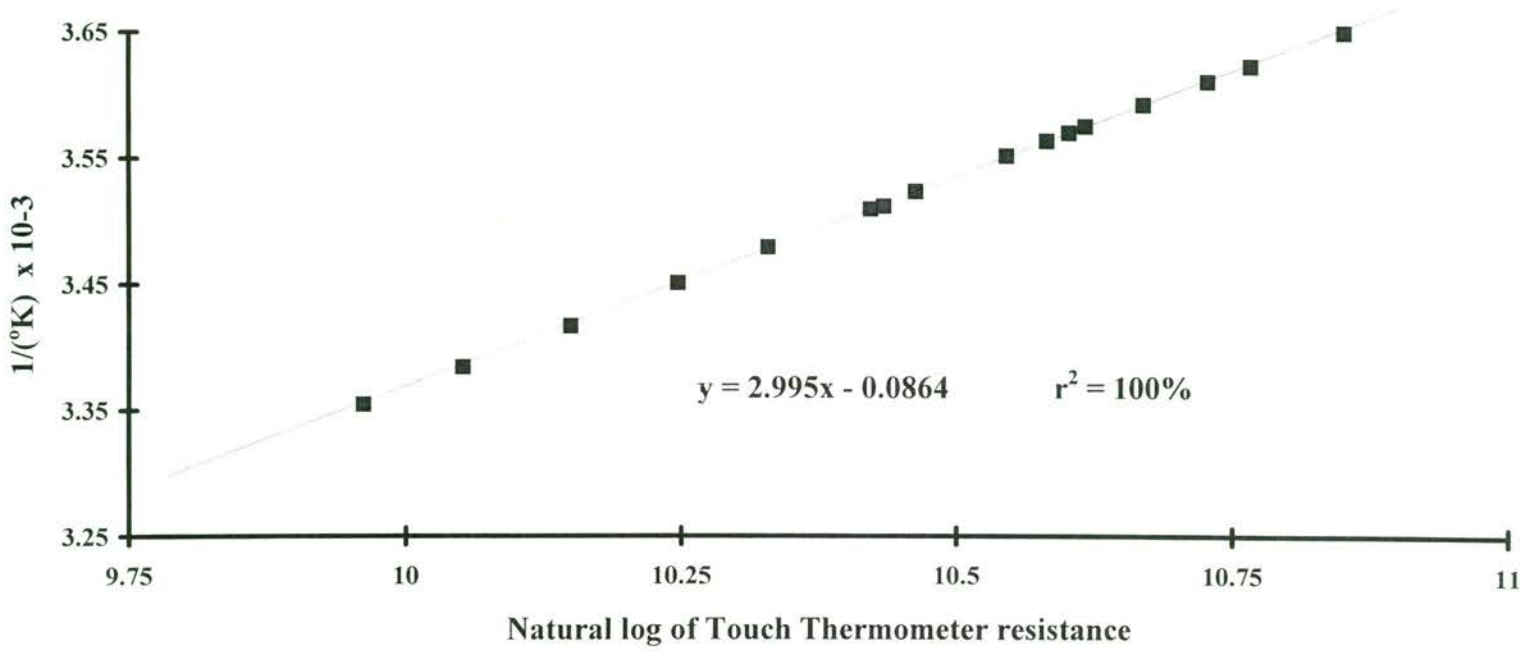


Figure A3.4; The relationship between 1/Reference temperature (°K) and the Touch Thermometer resistance reading (ohms) transformed to natural log.



Appendix 3.8a; **The effect of a 10 minutes saturation of the hair coat of the back and rump of ponies on their metabolic rate, heart rate and rectal and surface temperatures (^{o}C) over a period of 180 minutes compared with the dry state.**

Animal 1 Replicate 1

	Time (min)	Metab. rate (J/kg/s)	Heart rate (beats/min)		Rectal temp. (^{o}C)	Surface temperatures (^{o}C)					
						Neck (Dry)		Back(Wet)		Rump (Wet)	
			mean	(+/-s.e.)		H/A	S/H	H/A	S/H	H/A	S/H
Wet	0	1.71	50.3	(5.62)							
Drip	10	1.56	38.0	(5.50)	*	*	*	*	*	*	*
	44	1.42	36.6	(2.68)	*	*	13.2	*	13.2	*	13.2
	68	1.24	37.5	(3.60)	*	*	*	*	13.2	*	*
	123	1.36	*	*	*	16.9	28.2	13.2	21.8	11.4	20.8
	178	1.23	*	*	*	17.7	27.1	16.1	21.4	12.2	19.5
Dry		1.47	37.5	(5.34)	*	*	*	*	*	*	*

Water temperature 4.65 ^{o}C Water flowrate 8.99 l/min
Air temperature:- Dry 4 ^{o}C, Wet 2 ^{o}C
Relative Humidity 67 %

S/H = skin/hair interface H/A = hair/air interface Metab. rate = metabolic rate
N.B. The neck was never wetted.
* = missing data

Appendix 3.8b; **The effect of a 10 minutes saturation of the hair coat of the back and rump of ponies on their metabolic rate, heart rate and rectal and surface temperatures (^{o}C) over a period of 180 minutes compared with the dry state.**

Animal 3 Replicate 1

	Time (min)	Metab. rate (J/kg/s)	Heart rate (beats/min) mean (+/-s.e.)	Rectal temp. (^{o}C)	Surface temperatures (^{o}C) Neck (Dry)		Back(Wet)		Rump (Wet)	
					H/A	S/H	H/A	S/H	H/A	S/H
Wet	0	1.43	37.7 (2.10)							
Drip	10	1.40	37.6 (4.31)	*	*	*	*	*	*	*
	33	1.41	37.5 (2.80)	*	8.7	26.8	17.1	24.1	14.6	22.4
	93	1.54	* *	*	9.1	28.4	15.9	26.2	12.2	21.8
	138	1.44	* *	*	10.3	28.7	15.7	25.5	11.4	20.6
		stopped, pony agitated.								
Dry		1.42	36.7 (1.30)	*	*	*	8.4	29.5	11.1	31.6

Water temperature 4.25 ^{o}C Water flowrate 7.51 l/min
Air temperature:- Dry 3 ^{o}C, Wet 1.5 ^{o}C
Relative Humidity 74 %

S/H = skin/hair interface H/A = hair/air interface Metab. rate = metabolic rate
N.B. The neck was never wetted.
* = missing data

<u>Appendix 3.8c;</u> **The effect of a 10 minutes saturation of the hair coat of the back and rump of ponies on their metabolic rate, heart rate and rectal and surface temperatures (^{o}C) over a period of 180 minutes compared with the dry state.**

Animal 1 Replicate 2

	Time (min)	Metab. rate (J/kg/s)	Heart rate (beats/min) mean (+/-s.e.)	Rectal temp. (^{o}C)	Surface temperatures (^{o}C) Neck (Dry) H/A	Neck (Dry) S/H	Back(Wet) H/A	Back(Wet) S/H	Rump (Wet) H/A	Rump (Wet) S/H
Wet	0	1.47	36.1 (2.00)							
Drip	10	1.42	35.4 (1.20)	37.9	16.3	28.7	14.1	18.0	14.6	18.4
	58	1.22	35.2 (2.78)	37.9	16.3	32.2	14.6	22.4	15.7	20.8
	121	1.16	38.7 (2.30)	37.8	22.0	33.1	17.3	24.5	15.9	22.0
	181	1.26	38.4 (3.46)	37.8	15.7	31.1	16.9	21.3	15.4	21.4
Dry		1.31	37.0 (1.63)	37.9	23.3	32.6	11.1	28.7	20.2	29.7

Water temperature 4.9 ^{o}C Water flowrate 9.07 l/min
Air temperature:- Dry 7 ^{o}C, Wet 4.75 ^{o}C
Relative Humidity 71 %

S/H = skin/hair interface H/A = hair/air interface Metab. rate = metabolic rate
N.B. The neck was never wetted.

Appendix 3.8d; **The effect of a 10 minutes saturation of the hair coat of the back and rump of ponies on their metabolic rate, heart rate and rectal and surface temperatures (^{o}C) over a period of 180 minutes compared with the dry state.**

Animal 3 Replicate 2

	Time (min)	Metab. rate (J/kg/s)	Heart rate (beats/min) mean (+/-s.e.)	Rectal temp. (^{o}C)	Surface temperatures (^{o}C) Neck (Dry)		Back(Wet)		Rump (Wet)	
					H/A	S/H	H/A	S/H	H/A	S/H
Wet	0	1.56	35.1 (2.27)							
Drip	10	1.47	33.2 (1.91)	38.0	16.9	33.5	12.2	20.6	15.4	21.8
	60	1.49	36.7 (5.48)	37.9	19.9	34.3	20.9	24.5	19.2	25.8
	122	1.62	33.3 (3.37)	37.8	17.5	33.9	18.4	23.7	15.0	21.3
	180	1.54	32.5 (2.76)	37.9	17.3	32.0	18.1	22.8	17.1	23.3
Dry		1.50	32.0 (2.45)	38.0	18.4	32.0	25.5	26.8	14.6	30.2

Water temperature 4.55 ^{o}C Water flowrate 8.03 l/min
Air temperature:- Dry 6 ^{o}C, Wet 4 ^{o}C
Relative Humidity 70 %

S/H = skin/hair interface H/A = hair/air interface Metab. rate = metabolic rate
N.B. The neck was never wetted.

Appendix 3.8e; **The effect of a 10 minutes saturation of the hair coat of the back and rump of ponies on their metabolic rate, heart rate and rectal and surface temperatures (^{o}C) over a period of 180 minutes compared with the dry state.**

Animal 1 Replicate 3

	Time (min)	Metab. rate (J/kg/s)	Heart rate (beats/min) mean (+/-s.e.)	Rectal temp. (^{o}C)	Surface temperatures (^{o}C)					
					Neck (Dry)		Back(Wet)		Rump (Wet)	
					H/A	S/H	H/A	S/H	H/A	S/H
Wet	0	1.59	37.8 (6.51)							
Drip	5	1.43	35.7 (1.63)	37.8	16.7	29.5	15.0	19.2	14.4	18.6
	61	1.44	33.5 (2.76)	38.0	16.1	30.2	18.1	22.9	18.6	21.8
	101	1.43	36.2 (2.57)	37.8	17.3	30.9	17.8	21.8	16.7	22.0
Dry		1.44	35.0 (1.35)	37.8	21.0	30.9	14.6	30.9	17.8	30.2

Water temperature 5.25 ^{o}C Water flowrate 9.80 l/min
Air temperature:- Dry 9.5 ^{o}C, Wet 7 ^{o}C
Relative Humidity 67.5 %

S/H = skin/hair interface H/A = hair/air interface Metab. rate = metabolic rate
N.B. The neck was never wetted.

Appendix 3.8f; **The effect of a 10 minutes saturation of the hair coat of the back and rump of ponies on their metabolic rate, heart rate and rectal and surface temperatures (^{o}C) over a period of 180 minutes compared with the dry state.**

Animal 3 Replicate 3

	Time (min)	Metab. rate (J/kg/s)	Heart rate (beats/min) mean (+/-s.e.)	Rectal temp. (^{o}C)	Surface temperatures (^{o}C) Neck (Dry) H/A	Neck (Dry) S/H	Back(Wet) H/A	Back(Wet) S/H	Rump (Wet) H/A	Rump (Wet) S/H
Wet	0	1.45	33.8 (2.81)							
Drip	9	1.43	33.0 (2.27)	38.0	17.8	33.1	19.3	23.7	17.5	23.3
	46	1.48	34.0 (3.00)	38.0	22.0	33.5	19.9	27.0	22.8	28.2
	97	1.50	* *	37.8	12.4	31.6	20.8	27.6	18.0	28.2
	154	1.47	37.0 (5.02)	38.0	22.1	32.0	19.9	28.2	19.9	26.8
Dry		1.45	32.8 (1.65)	37.8	12.7	32.2	23.0	33.1	22.4	33.1

Water temperature 5.75 ^{o}C Water flowrate 7.23 l/min
Air temperature:- Dry 8 ^{o}C, Wet 5.5 ^{o}C
Relative Humidity 66 %

S/H = skin/hair interface H/A = hair/air interface Metab. rate = metabolic rate
N.B. The neck was never wetted.
* = missing data

<u>Appendix 3.8g;</u> **The effect of a 10 minutes saturation of the hair coat of the back and rump of ponies on their metabolic rate, heart rate and rectal and surface temperatures (^{o}C) over a period of 180 minutes compared with the dry state.**

Animal 1 Replicate 4

	Time (min)	Metab. rate (J/kg/s)	Heart rate (beats/min) mean (+/-s.e.)	Rectal temp. (^{o}C)	Surface temperatures (^{o}C) Neck (Dry) H/A	Neck (Dry) S/H	Back(Wet) H/A	Back(Wet) S/H	Rump (Wet) H/A	Rump (Wet) S/H
Wet	0	1.20	34.1 (6.11)							
Drip	7	1.16	32.9 (5.07)	37.9	9.4	32.0	15.7	21.3	16.1	23.7
	60	1.03	33.6 (3.20)	38.0	11.7	32.0	12.2	19.5	13.2	22.0
	130	0.94	33.5 (4.13)	37.9	11.7	32.0	14.1	20.1	15.0	23.7
	178	1.05	33.7 (1.80)	37.9	12.4	30.4	12.2	21.4	12.2	20.2
Dry		1.16	33.5 (2.16)	37.7	22.8	34.3	15.4	31.6	22.8	31.6

Water temperature 5.5 ^{o}C Water flowrate 6.53 l/min
Air temperature:- Dry 3.5 ^{o}C, Wet 0.5 ^{o}C
Relative Humidity 50 %

S/H = skin/hair interface H/A = hair/air interface Metab. rate = metabolic rate
N.B. The neck was never wetted.

Appendix 3.8h; **The effect of a 10 minutes saturation of the hair coat of the back and rump of ponies on their metabolic rate, heart rate and rectal and surface temperatures (^{o}C) over a period of 180 minutes compared with the dry state.**

Animal 3 Replicate 4

	Time (min)	Metab. rate (J/kg/s)	Heart rate (beats/min) mean (+/-s.e.)	Rectal temp. (^{o}C)	Surface temperatures (^{o}C) Neck (Dry) H/A	Neck (Dry) S/H	Back(Wet) H/A	Back(Wet) S/H	Rump (Wet) H/A	Rump (Wet) S/H
Wet	0	1.45	33.3 (1.07)							
Drip	10	1.43	33.0 (1.73)	37.8	10.6	32.2	13.9	22.0	15.2	22.0
	60	1.42	33.4 (3.91)	37.9	12.0	32.0	17.5	24.8	17.5	23.3
	120	1.37	31.9 (0.67)	37.9	8.7	31.6	16.3	20.8	15.7	22.8
	180	1.41	33.1 (4.72)	37.9	17.5	33.5	14.3	22.1	20.6	22.1
Dry		1.48	32.6 (1.95)	37.8	13.4	32.0	20.1	32.2	20.9	30.9

Water temperature 5.6 ^{o}C Water flowrate 7.05 l/min
Air temperature:- Dry 2 ^{o}C, Wet 0 ^{o}C
Relative Humidity 64 %

S/H = skin/hair interface H/A = hair/air interface Metab. rate = metabolic rate
N.B. The neck was never wetted.

Appendix 3.9; Simplification of the formula (Webster, 1974) for the calculation of lower critical temperature (LCT).

$$LCT = Tb + 17\left(\frac{Ts - Ta}{M-17}\right) - M\left(\frac{Tb-Ts}{M} + \frac{Ts-Ta}{M-17}\right)$$

$$LCT = Tb + 17\left(\frac{Ts}{M-17} - \frac{Ta}{M-17}\right) - M\left(\frac{Tb}{M} - \frac{Ts}{M} + \frac{Ts}{M-17} - \frac{Ta}{M-17}\right)$$

$$LCT = Tb + \frac{17Ts}{M-17} - \frac{17Ta}{M-17} - \frac{MTb}{M} + \frac{MTs}{M} - \frac{MTs}{M-17} + \frac{MTa}{M-17}$$

$$LCT = (Tb - Tb) + Ts + \frac{17Ts}{M-17} - \frac{17Ta}{M-17} - \frac{MTs}{M-17} + \frac{MTa}{M-17}$$

$$LCT = Ts + \left(\frac{17Ts - 17Ta - MTs + MTa}{M-17}\right)$$

$$LCT = Ts + \frac{\{Ts(17-M) - Ta(17-M)\}}{M-17}$$

$$LCT = Ts - \frac{\{Ts(M-17) - Ta(M-17)\}}{M-17}$$

$$LCT = (Ts - Ts) + Ta$$

LCT = Ta = ambient temperature.

Appendix 4.1;

A description of the area (m^2) and topography (gradient and direction of slope) of each quadrat in the study field.

Quadrat	*area (m^2)*	*gradient (%)*	*facing**
D1	4400	8.6	ESE
D2	7055	16.3	ENE
D3	9330	13.2	ENE
D4	8894	8.0	ENE
T1	12297	10.1	W
T2	10397	3.6	SW
T3	11783	3.2	SSW
T4	10000	0.0	0
T5	10000	11.4	E
T6	10532	9.4	E
T7	5049	7.1	E
Q1	8022	7.1	W
Q2	10000	4.9	W
Q3	10000	3.6	SW
Q4	10000	10.6	SE
Q5	7228	12.7	E
B1	5241	6.7	SW
B2	12511	4.48	SSW
B3	7970	4.37	S
B4	2960	13.52	S
Total area	173651		

* = compass bearings; North, East, South, West.

Appendix 4.2;

The observation schedules for the winter (Table A4.1) and summer (Table A4.2) periods.

Table A4.1;

				March									April		
Start time	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5
00:00			■					■					■		
02:00				■					■						■
04:00			■					■					■		
06:00		■					■					■			
08:00	■					■					■				
10:00					■		■					■			
12:00	■					■					■				
14:00		■					■					■			
16:00	■					■					■				
18:00			■		■			■					■		
20:00				■					■					■	
22:00			■		■			■					■		

Table A4.2;

						JULY						
Start time	11	12	13	14	15	16	17	18	19	20	21	22
00:00					■		■				■	
02:00						■		■				■
04:00					■		■				■	
06:00		■		■						■		
08:00	■		■						■			
10:00		■		■						■		
12:00	■		■						■			
14:00		■		■						■		
16:00			■			■			■			
18:00					■		■				■	
20:00						■		■				■
22:00					■		■				■	

Appendix 4.3;

The number of observations (scan samples) of 7 behaviour categories in each hour of the day in winter. The sum of 3 composite days. Final total adjusted for missed observations

Time	ingest	move	stand	lie	interact	other	TOTAL		
00:00	53	1	13	2	2	1	72		
01:00	38	0	30	2	1	1	72		
02:00	16	0	13	7	0	0	36	36 missing	
03:00	22	0	21	5	0	0	48	24 missing	
04:00	48	1	13	10	0	0	72		
05:00	45	0	27	0	0	0	72		
06:00	63	1	4	2	0	2	72		
07:00	68	0	1	3	0	0	72		
08:00	55	0	13	0	0	4	72		
09:00	24	2	44	0	0	2	72		
10:00	52	3	1	9	0	1	66	6 missing	
11:00	68	4	0	0	0	0	72		
12:00	52	5	11	4	0	0	72		
13:00	48	0	13	5	0	0	66	6 missing	
14:00	49	2	16	4	0	1	72		
15:00	57	3	10	2	0	0	72		
16:00	56	0	16	0	0	0	72		
17:00	63	2	6	0	0	1	72		
18:00	71	1	0	0	0	0	72		
19:00	69	2	1	0	0	0	72		
20:00	39	2	16	15	0	0	72		
21:00	46	2	8	16	0	0	72		
22:00	27	0	20	0	0	1	48	24 missing	
23:00	45	1	0	0	0	2	48	24 missing	
TOTAL	1174	32	297	86	3	16	1608		
+	63	1	34	9		1	108	123	missing
adjusted total	1237	33	331	95	3	14	1716	15 missing	

missing = observation not recorded

Appendix 4.3;/cont.

The number of observations (scan samples) of 7 behaviour categories in each hour of the day in the summer. The sum of 3 composite days.

Time	ingest	move	stand	lie	interact	other	TOTAL	
00:00	32	2	31	3	2	0	70	2 OS
01:00	27	8	24	8	0	5	72	
02:00	37	1	29	3	2	0	72	
03:00	24	0	15	29	2	2	72	
04:00	49	3	7	5	1	1	66	6 missing
05:00	34	4	17	13	2	2	72	
06:00	45	3	10	8	1	5	72	
07:00	48	7	7	6	4	0	72	
08:00	40	6	12	5	0	3	66	6 missing
09:00	32	3	31	2	3	1	72	
10:00	45	3	13	0	0	11	72	
11:00	22	0	46	0	0	4	72	
12:00	37	3	29	0	2	1	72	
13:00	35	8	24	0	0	5	72	
14:00	47	13	10	0	1	1	72	
15:00	40	2	29	0	0	1	72	
16:00	30	0	37	0	0	5	72	
17:00	57	8	6	0	0	1	72	
18:00	54	0	15	0	0	3	72	
19:00	57	3	9	0	1	2	72	
20:00	54	1	1	4	9	3	72	
21:00	51	3	0	2	0	4	60	12 missing
22:00	47	2	13	0	1	3	66	6 missing
23:00	26	3	29	9	0	5	72	
TOTAL	970	86	444	97	31	68	1696	

OS = pony out of sight

missing = observation not recorded

Appendix 4.4;

Distance (m) travelled in the winter according to quadrat locations — Mean daily distance = 3122.7 (s.e. 188.36) m — n = 18

* missing values replaced by the mean value for the equivalent time during the other two 24 h periods

Day1	Time of day											
Pony	0	*2	4	6	8	10	12	14	16	18	20	22	Total 1
Beauty	0	150	100	482.8	0	500	300	100	200	400	0	0	2232.8
Brandy	0	100	100	747.8	414.4	300	241.4	100	200	500	0	0	2703.6
Browny	0	0	100	382.8	241.4	500	241.4	100	200	300	0	0	2065.6
Friendly	0	200	100	641.4	200	400	100	100	0	400	0	0	2141.4
Trim	0	50	100	602	241.4	300	341.4	100	423.6	300	0	0	2458.4
Tufty	0	50	100	865	100	665	100	100	100	300	0	0	2380

Day2	Time of day												
Pony	0	2	4	6	8	10	12	14	16	18	20	22	Total 2
Beauty	200	300	241.4	0	100	341.4	582.8	500	200	341.4	341.4	341.4	3148.4
Brandy	341.4	200	100	341.4	323.6	300	141.4	200	241.4	100	300	241.4	2589.2
Browny	400	0	100	100	300	200	441.4	441.4	300	400	200	300	2882.8
Friendly	200	400	0	200	241.4	341.4	341.4	824.2	100	300	200	200	3148.4
Trim	341.4	100	100	0	200	200	482.8	341.4	465	300	341.4	341.4	2872
Tufty	200	100	100	200	300	341.4	341.4	682.8	300	441.4	200	141.4	3207

Day3	Time of day												
Pony	0	2	4	6	8	10	12	14	16	18	20	*22	Total 3
Beauty	100	0	241.4	441.4	341.4	788.6	441.4	523.6	641.4	641.4	600	170.7	4831.3
Brandy	0	0	100	700	241.4	141.4	424.2	523.6	700	582.8	500	120.7	4034.1
Browny	100	0	241.4	741.4	341.4	724.2	200	424.2	423.6	0	482.8	150	3729
Friendly	0	0	300	682.8	141.4	323.6	141.4	460.6	500	582.8	441.4	100	3674
Trim	241.4	0	241.4	541.4	300	423.6	441.4	560.6	423.6	700	600	170.7	4402.7
Tufty	0	0	241.4	400	241.4	323.6	441.4	424.2	500	482.8	582.8	70.7	3708.3

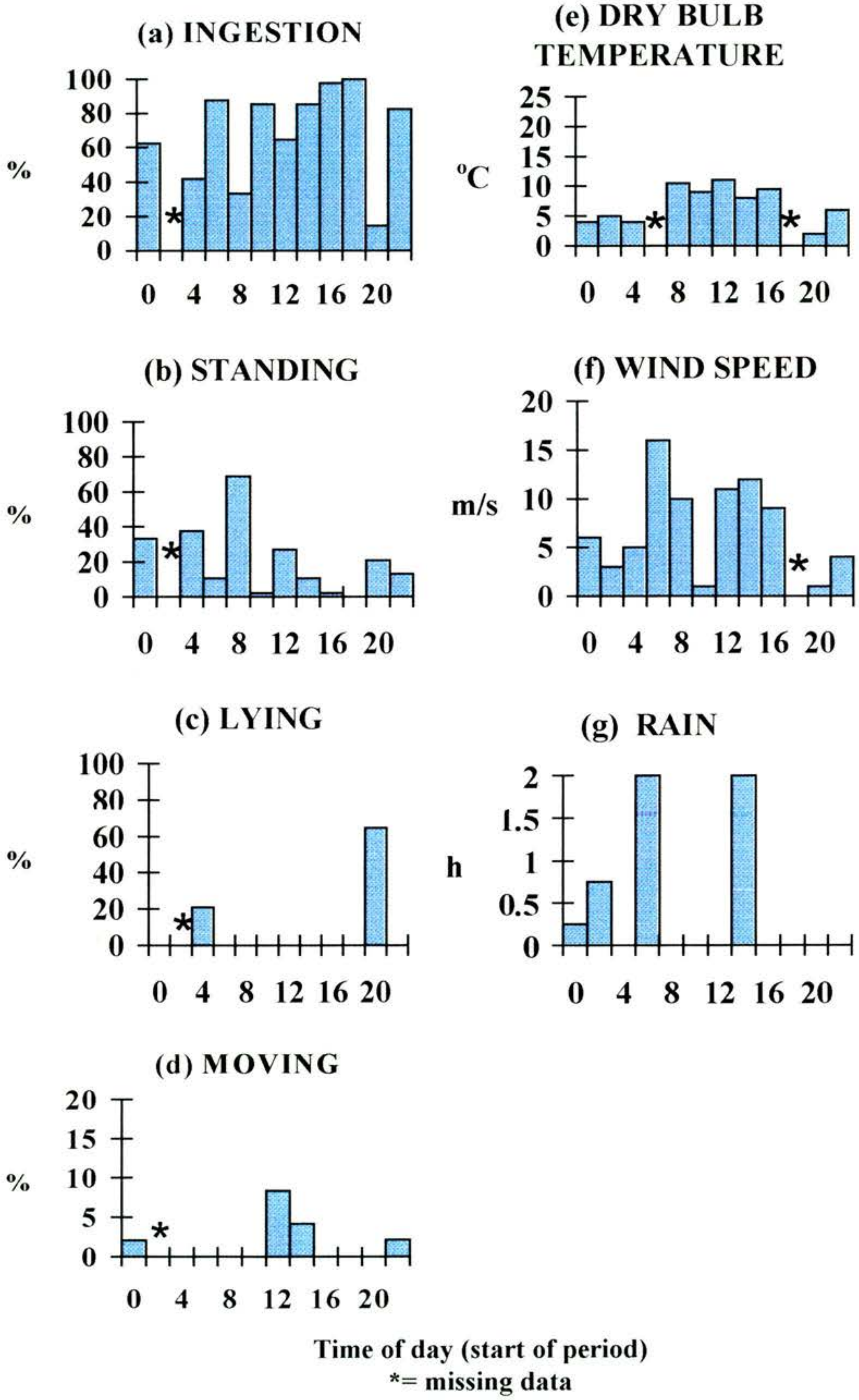
Appendix 4.4/cont.

Distance (m) travelled in the summer according to quadrat locations Mean daily distance = 3749.0 (s.e. 163.6) m n = 18

Day1	Time of day											
Pony	0	2	4	6	8	10	12	14	16	18	20	22	Total 1
Beauty	541.4	200.0	665.0	300.0	100.0	400.0	682.8	200.0	706.4	300.0	200.0	541.4	4837.0
Brandy	300.0	300.0	241.4	541.4	100.0	441.4	782.8	200.0	643.4	200.0	341.4	523.6	4615.4
Browny	441.4	100.0	223.6	300.0	100.0	400.0	782.8	341.4	643.4	300.0	300.0	341.4	4274.0
Friendly	300.0	100.0	241.4	300.0	100.0	400.0	1118.0	200.0	643.4	200.0	300.0	541.4	4444.2
Trim	441.4	100.0	241.4	300.0	100.0	500.0	682.8	300.0	699.0	241.4	100.0	600.0	4306.0
Tufty	300.0	200.0	241.4	441.4	100.0	341.4	765.0	300.0	699.0	341.4	441.4	323.6	4494.6
Day2	Time of day											
Pony	0	2	4	6	8	10	12	14	16	18	20	22	Total 2
Beauty	0.0	141.4	0.0	400.0	0.0	200.0	441.4	539.8	516.2	441.4	341.4	141.4	3163.0
Brandy	0.0	100.0	0.0	300.0	0.0	400.0	300.0	632.4	657.6	400.0	100.0	200.0	3090.0
Browny	0.0	223.6	0.0	300.0	241.4	341.4	616.2	639.8	516.2	241.4	300.0	141.4	3561.4
Friendly	0.0	100.0	0.0	200.0	0.0	200.0	300.0	639.8	516.2	441.4	100.0	141.4	2638.8
Trim	0.0	100.0	200.0	323.6	200.0	200.0	300.0	539.8	657.6	441.4	100.0	141.4	3203.8
Tufty	0.0	100.0	0.0	423.6	0.0	200.0	341.4	539.8	516.2	441.4	400.0	141.4	3103.8
Day3	Time of day											
Pony	0	2	4	6	8	10	12	14	16	18	20	22	Total 3
Beauty	641.4	441.4	200.0	500.0	516.2	0.0	0.0	657.6	141.4	241.4	500.0	300.0	4139.4
Brandy	341.4	300.0	100.0	441.4	223.6	0.0	0.0	423.6	141.4	323.6	482.8	0.0	2777.8
Browny	241.4	241.4	341.4	765.0	416.2	0.0	0.0	657.6	141.4	300.0	382.8	100.0	3587.2
Friendly	641.4	241.4	100.0	200.0	323.6	0.0	0.0	600.0	141.4	423.6	400.0	0.0	3071.4
Trim	782.8	341.4	200.0	541.4	316.2	0.0	0.0	657.6	141.4	323.6	600.0	0.0	3904.4
Tufty	682.8	582.8	0.0	565.0	516.2	0.0	0.0	657.6	141.4	423.6	500.0	200.0	4269.4

Appendix 4.5;

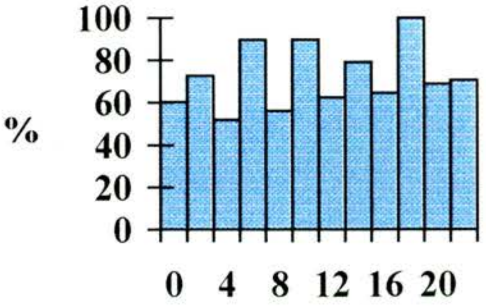
Figure A4.3; The proportion (%) of four activities and the prevailing weather conditions during each two hour period of the first winter "day" of observation.



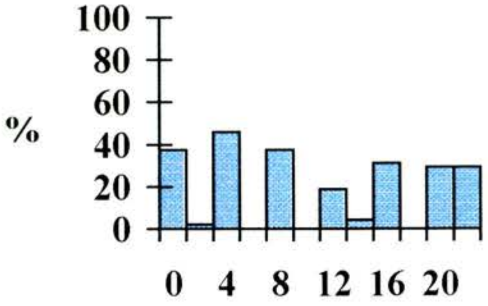
Appendix 4.5/cont.

Figure A4.4; The proportion (%) of four activities and the prevailing weather conditions during each two hour period of the second winter "day" of observation.

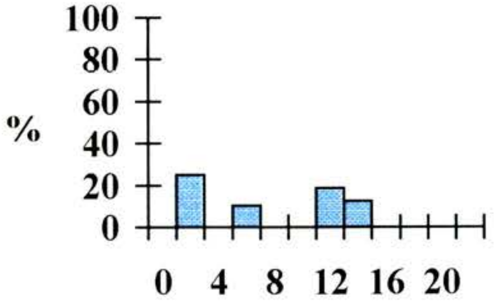
(a) INGESTION



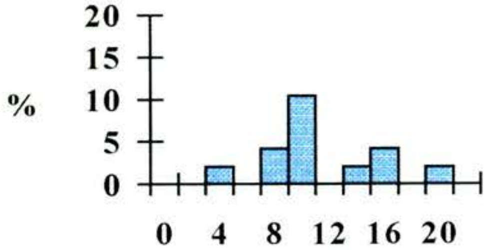
(b) STANDING



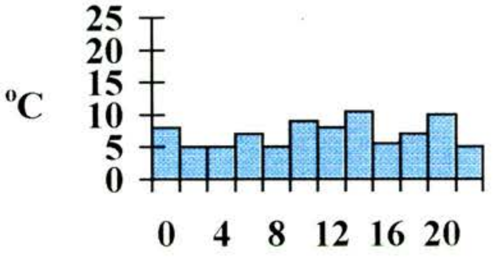
(c) LYING



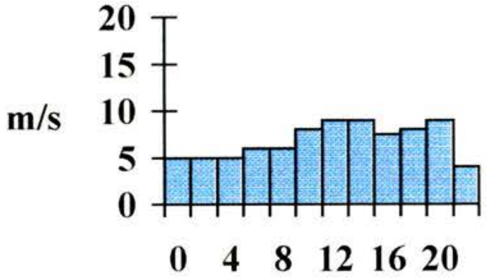
(d) MOVING



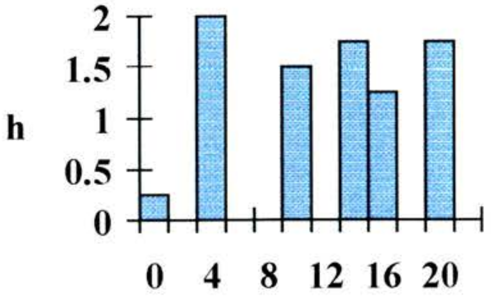
(e) DRY BULB TEMPERATURE



(f) WIND SPEED



(g) RAIN

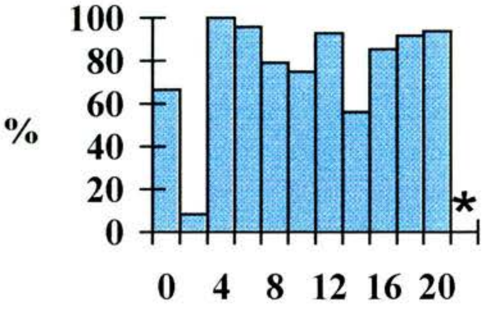


Time of day (start of period)

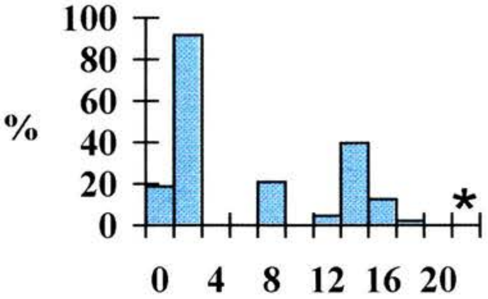
Appendix 4.5/cont.

Figure A4.5; The proportion (%) of four activities and the prevailing weather conditions during each two hour period of the third winter "day" of observation.

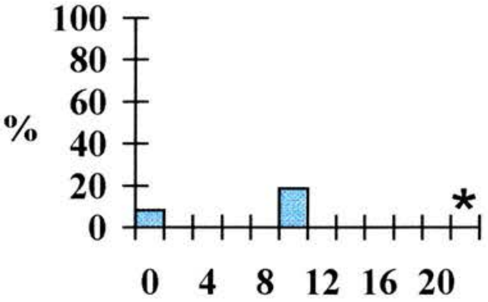
(a) INGESTION



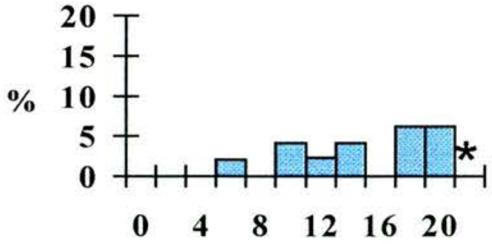
(b) STANDING



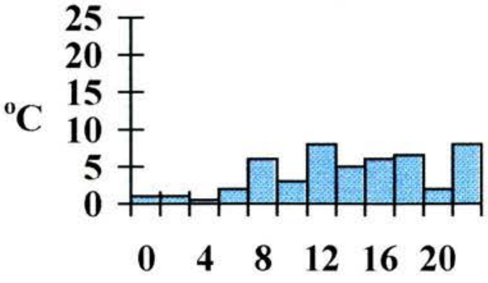
(c) LYING



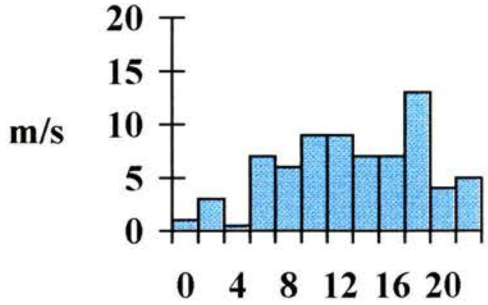
(d) MOVING



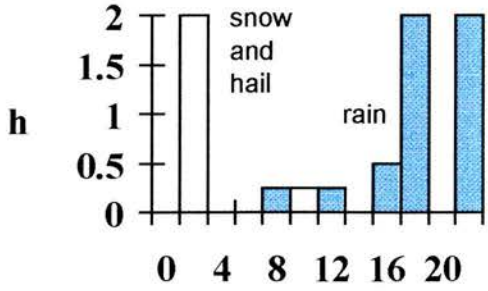
(e) DRY BULB TEMPERATURE



(f) WIND SPEED



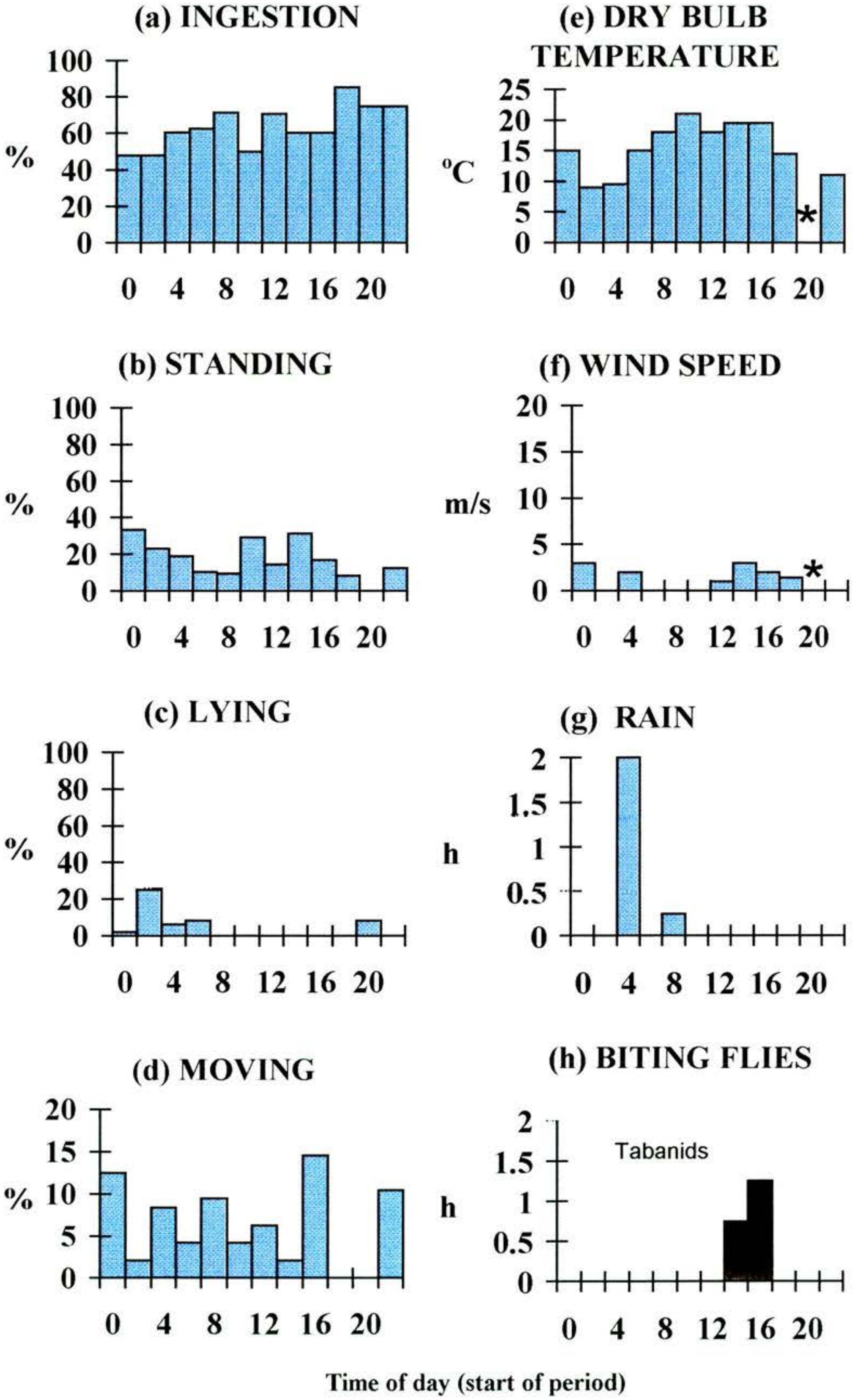
(g) RAIN



Time of day (start of period)
* = missing data

Appendix 4.5/cont.

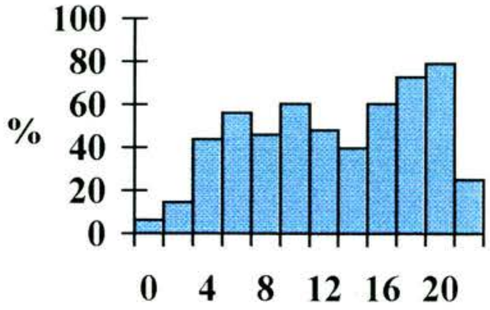
Figure A4.6; The proportion (%) of four activities and the prevailing weather conditions during each two hour period of the first summer "day" of observation.



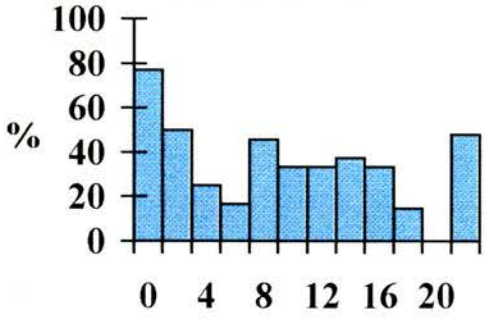
Appendix 4.5/cont.

Figure A4.7; The proportion (%) of four activities and the prevailing weather conditions during each two hour period of the second summer "day" of observation.

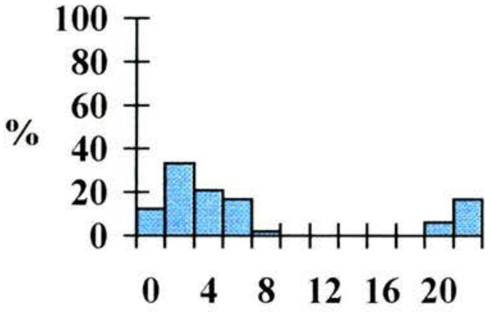
(a) INGESTION



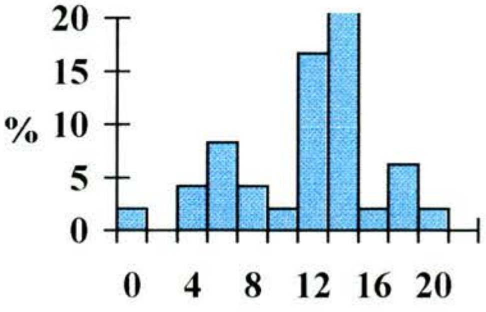
(b) STANDING



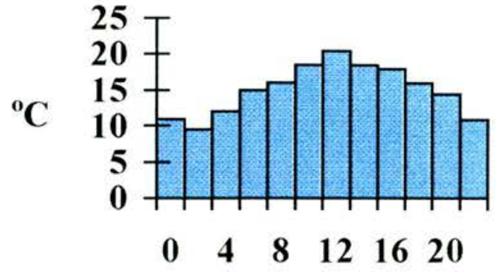
(c) LYING



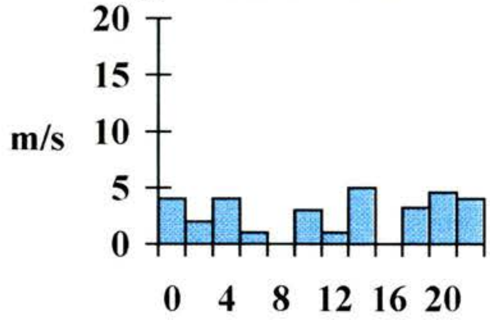
(d) MOVING



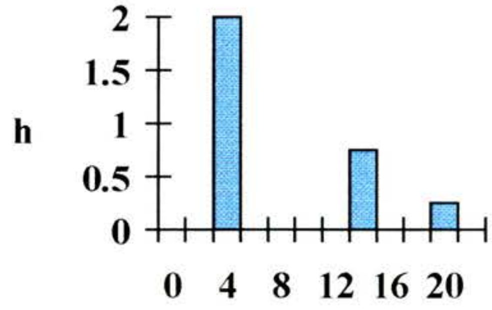
(e) DRY BULB TEMPERATURE



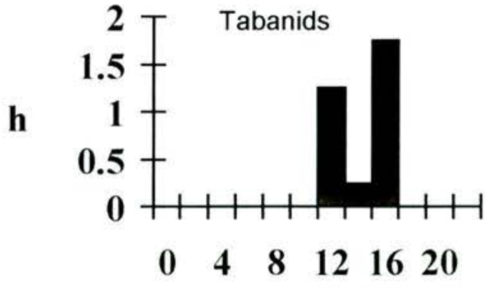
(f) WIND SPEED



(g) RAIN



(h) BITING FLIES



Time of day (start of period)

Appendix 4.6;

Environmental conditions during 72 hours of observation in the winter and summer.

Tables A4.3-4 and Figures A4.9-12 (on following pages)

Table A4.3;

Duration of precipitation; fly activity and clear skies

	Duration (hours)	
Climatic conditions	winter	summer
sunshine	11.00	31.00
clear night skies	6.25	8.00
dry & cloudy	34.50	26.25
mist or fog	1.25	1.25
drizzle	0.00	2.75
rain	16.75	0.50
snow or hail	2.25	0.00
Biting flies		
Tabanids		8.25
Culicoides		4.00

Table A4.4;

Duration and area of cloud cover

Cloud cover	duration (hours)	
%	winter	summer
0 (clear)	4.75	10.75
12.50	5.75	12.75
25.00	0.00	7.75
37.50	1.50	5.25
50.00	5.50	4.25
62.50	0.75	0.75
75.00	8.75	1.75
87.50	11.50	3.75
100.00	31.50	22.75

Figure A4.9:- Duration (hours) of different wind speeds in the summer and winter observation periods (total time 72 h).

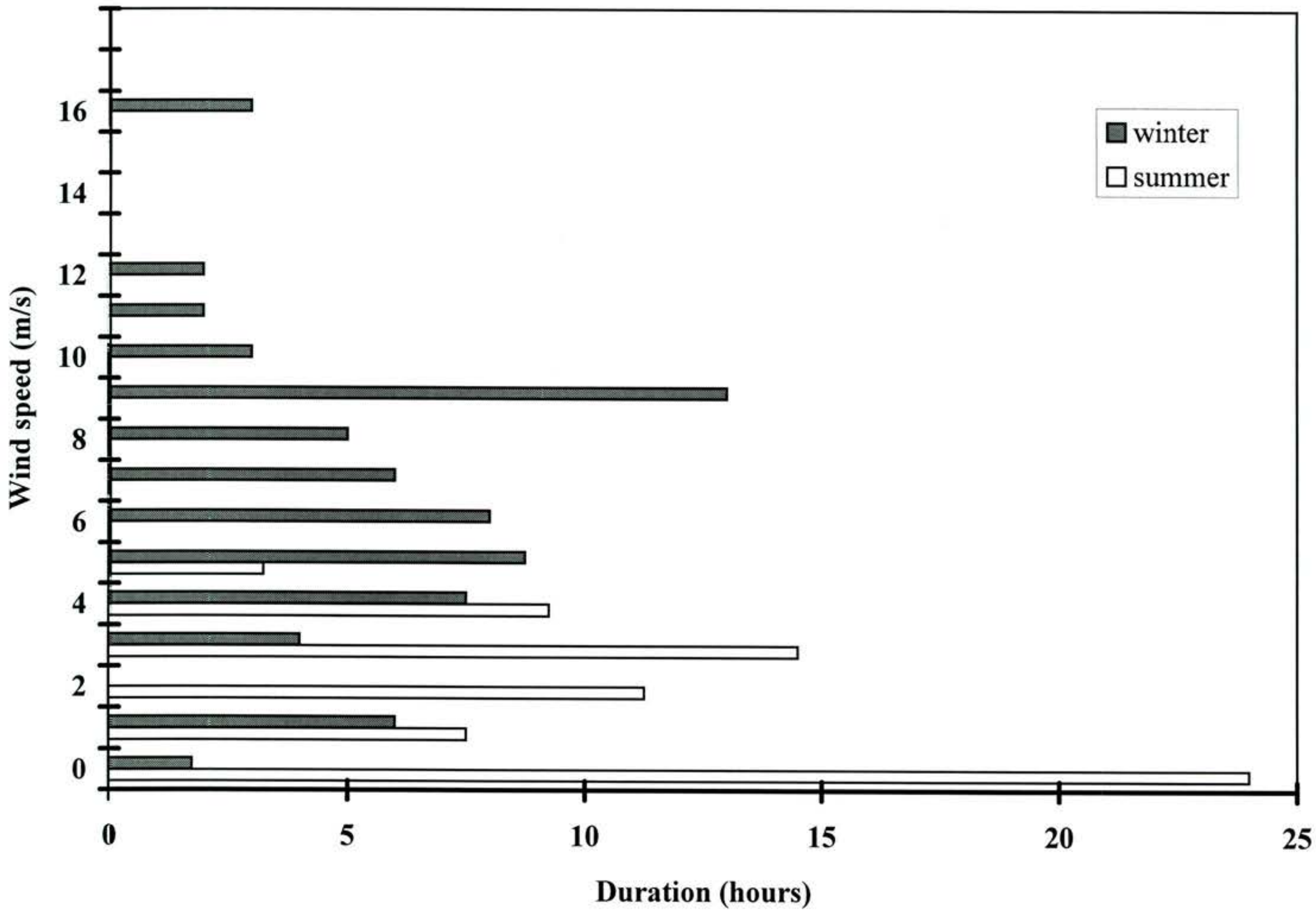


Figure A4.10:- Duration (hours out of 72) of different dry bulb temperatures (°C) in the summer and winter observation periods.

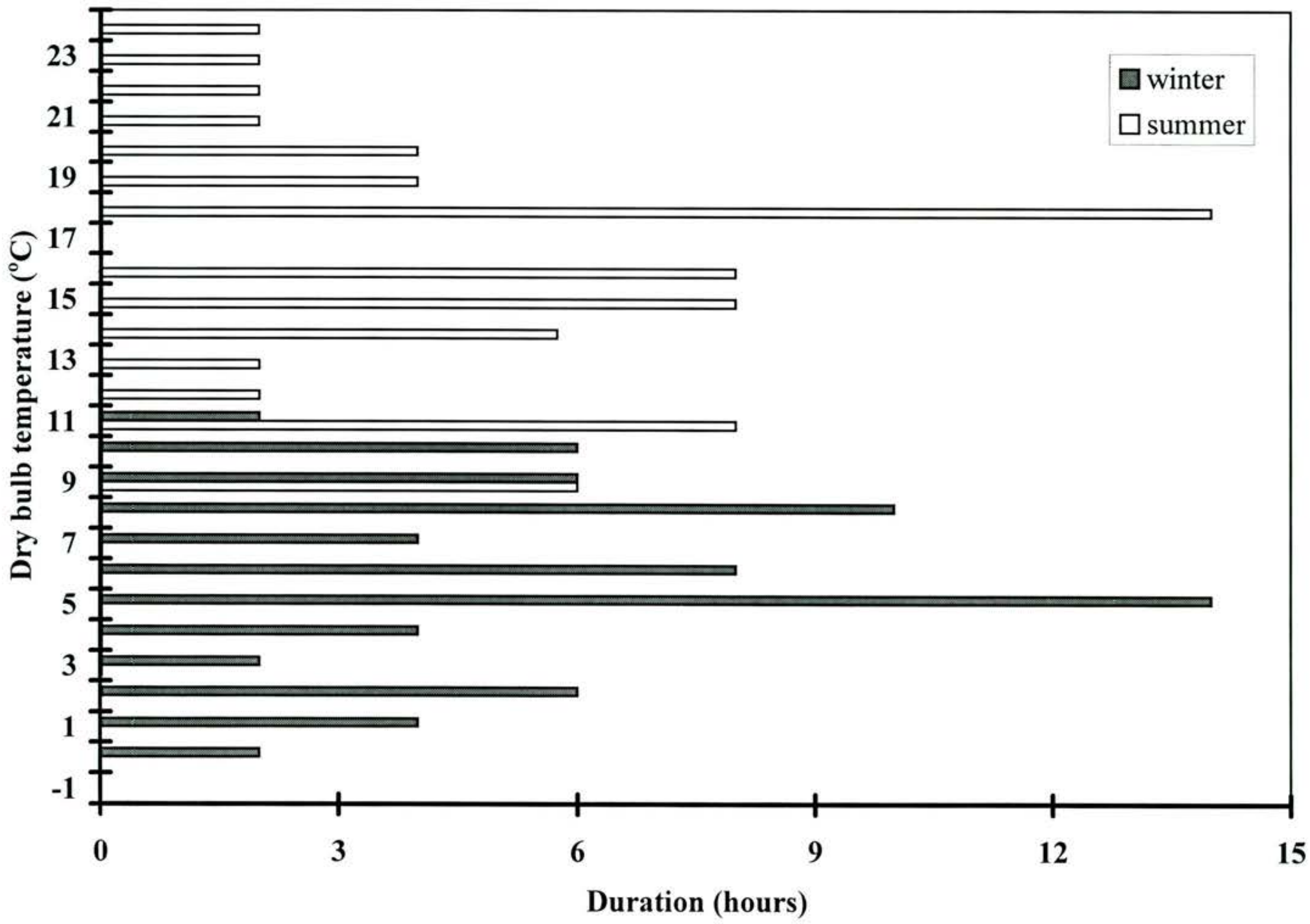


Figure A4.11:- Duration (hours out of 72) of different wet bulb temperatures (°C) in the summer and winter observation periods.

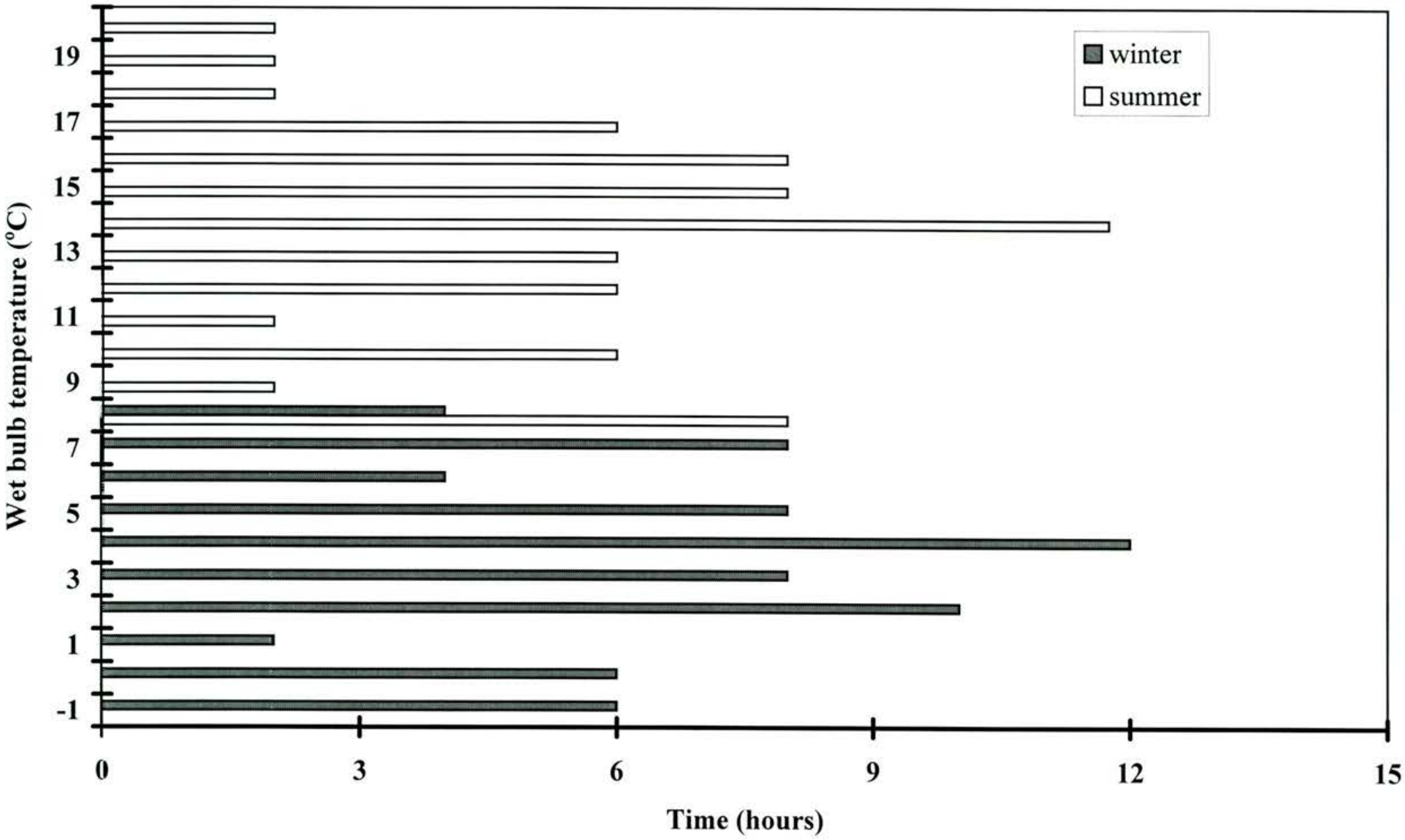
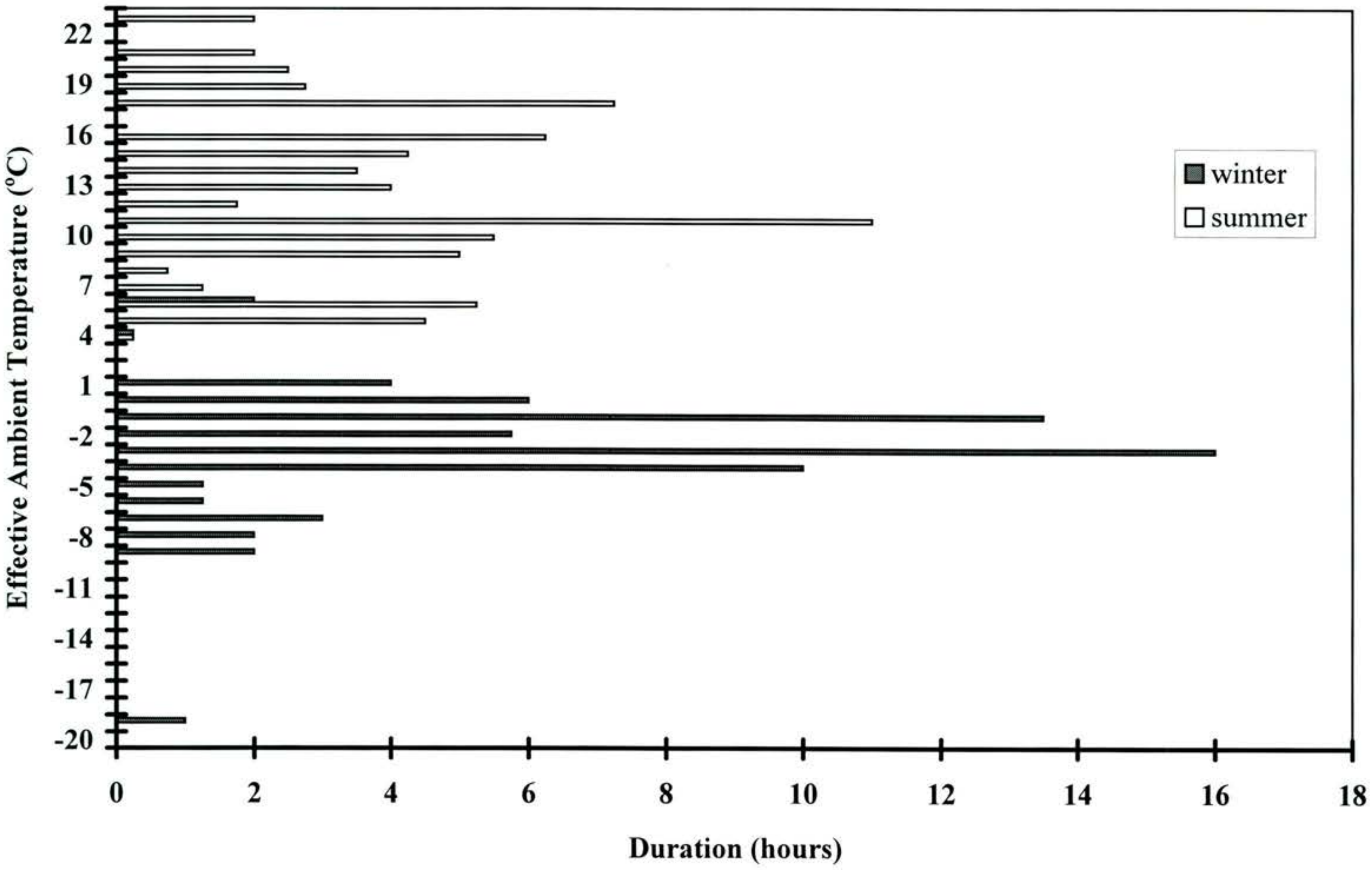


Figure A4.12:- **Duration (hours) of different Effective Ambient Temperatures (^{o}C) in the summer and winter observation periods (total time 72 h).**



Appendix 4.7; Total number of observations (total time = 72 hours) in each quadrat in winter and summer.

Table A4.5

Winter

1 observation = 1 pony in one 15 min scan

quad:at	ingest	move	stand	lie	interact	other	total obs
D1	28	1	0	0	0	0	29
D2	72	2	63	0	0	5	142
D3	56	2	4	0	0	0	62
D4	51	1	8	0	0	0	60
T1	163	1	43	17	2	2	228
T2	123	2	4	11	0	1	141
T3	49	2	18	0	0	0	69
T4	55	0	0	4	0	2	61
T5	65	2	14	9	0	0	90
T6	30	1	1	0	0	1	33
T7	4	0	0	0	0	0	4
Q1	66	1	21	34	1	1	124
Q2	108	2	0	0	0	0	110
Q3	29	0	0	0	0	0	29
Q4	40	2	1	2	0	0	45
Q5	46	8	7	9	0	0	70
B1	84	3	73	0	0	0	160
B2	62	2	5	0	0	0	69
B3	26	0	12	0	0	0	38
B4	17	0	23	0	0	1	41
TOTAL	1174	32	297	86	3	13	1605

123 missing observations

Appendix 4.7/cont.

Table A4.6

Summer

1 observation = 1 pony in one 15 min scan

quadrat	ingest	move	stand	lie	interact	other	total observations
D1	0	0	0	0	1	0	1
D2	2	0	0	0	0	0	2
D3	0	0	0	0	0	0	0
D4	0	0	0	0	0	0	0
T1	74	13	21	0	1	10	119
T2	77	5	7	6	2	8	105
T3	134	16	9	11	3	6	179
T4	207	11	223	7	8	16	472
T5	23	2	0	0	0	1	26
T6	25	3	72	24	2	6	132
T7	1	0	0	0	0	0	1
Q1	67	17	34	2	0	8	128
Q2	149	2	8	14	7	4	184
Q3	74	4	11	10	4	3	106
Q4	19	0	4	0	1	0	24
Q5	12	0	6	0	2	1	21
B1	34	4	14	0	0	1	53
B2	39	4	8	4	0	3	58
B3	27	3	26	19	0	0	75
B4	6	2	1	0	0	1	10
TOTAL	970	86	444	97	31	68	1696

32 missing observations

Appendix 4.8;		Orientation of ponies to the wind whilst grazing in winter and summer.										
Table A4.7a		Winter						Table A4.7b				
		Sum of observations over 72 hours										
wind speed		1 observation = one pony in one 15 min scan						as % of all observations within each wind speed category				
m/s	hindquarters	side	face	total				m/s	hindquarters	side	face	total
1	13	19	16	48				1	27.08	39.58	33.33	100.00
2	1	5	0	6				*2.5	33.33	55.56	11.11	100.00
*3	2	0	1	3				4	48.44	17.19	34.38	100.00
4	31	11	22	64				5	58.14	10.85	31.01	100.00
5	75	14	40	129				6	75.31	7.41	17.28	100.00
6	61	6	14	81				7	51.38	12.84	35.78	100.00
7	56	14	39	109				8	53.57	12.86	33.57	100.00
8	75	18	47	140				9	42.45	8.63	48.92	100.00
9	59	12	68	139				*10	42.00	0.00	58.00	100.00
10	8	0	10	18				16	91.30	0.00	8.70	100.00
*11	0	0	1	1								
16	21	0	2	23								
Total	402	99	260	761								
* as there were less than 4 observations at 3 and 11 m/s, these data were added to the next lowest wind speed.												

Appendix 4.8/cont.											
Table A4.8a		Summer					Table A4.8b				
		Sum of observations over 72 hours									
wind speed		1 observation = one pony in one 15 min scan					Sums as % of all observations within each wind speed category				
m/s	hindquarters	side	face	total			m/s	hindquarters	side	face	total
1	27	61	16	104			1	26.00	58.60	15.40	100
2	36	55	15	106			2	34.00	51.90	14.10	100
3	57	80	38	175			3	32.60	45.70	21.70	100
4	33	30	15	78			4	42.30	38.50	19.20	100
5	11	13	12	36			5	30.60	36.10	33.30	100
Total	164	239	96	499							

<u>Appendix 4.9</u>; **Mean (s.e.) or median (interquartile range) sward height (mm) in each quadrat measured in winter and summer, and for areas classified in summer as short, average, long and in rushes.**

Sward height (mm)

	Winter		*Summer*		*Summer*		
Quadrat	*mean (s.e.)*	*median (Q1-Q3)*	*mean (s.e.)*	*median (Q1-Q3)*	*classification*	*mean (s.e.)*	*median (Q1-Q3)*
T1	33.3 (2.58)		148.4 (7.52)		*short*		32.5 (30.0 - 39.4)
T2		40.0 (30 - 50)	129.3 (9.34)		*average*	92.62 (3.41)	
T3	51.0 (2.27)			87.5 (72.5 - 128.8)	*long*	171.1 (5.82)	
T4	47.9 (3.17)		77.8 (5.16)		*in rushes*	240.3 (7.41)	
T5			93.4 (5.40)				
T6				136.3 (110.0 - 178.1)			
T7				155.0 (112.5 - 233.7)			
Q1		36.3 (30 - 53.8)		68.8 (57.5 - 101.1)			
Q2	52.1 (4.04)						
Q3	49.8 (2.38)		122.0 (8.53)				
Q4			112.6 (7.73)				
Q5				80.0 (56.3 - 108.8)			
B1	44.6 (3.54)			55.0 (38.8 - 76.9)			
B2		40.0 (30.0 - 55.0)	124.4 (10.3)				
B3				100.0 (71.9 - 188.9)			
B4			85.3 (6.66)				
D1			108.8 (9.11)				
D2				95.0 (65.0 - 125.0)			
D3			119.1 (7.61)				
D4				198.8 (146.3 - 278.8)			