INGESTIVE BEHAVIOUR AND DIET SELECTION IN GRAZING CATTLE AND SHEEP

T. DAVID A. FORBES

Ph.D.

University of Edinburgh

1982

Abstract

Ingestive behaviour and diet selection in grazing cattle and sheep

T.D.A. Forbes University of Edinburgh.

A review of the literature suggested that the ingestive behaviour of grazing animals is largely determined by the structure and botanical composition of the sward, but little information is available from indigenous, temperate swards or for cattle and sheep grazing together. The following three grazing experiments were carried out to examine aspects of the responses of cattle and sheep to variations in sward conditions.

In the first, animal responses, in terms of ingestive behaviour and diet composition, to changes in the structure of sown swards were examined. In the second, the influence of the presence of dung of the same or the opposite species on grazing patterns and herbage utilisation in cattle and sheep, and hence on their complementarity of grazing was examined. In the third experiment the responses of cattle and sheep to indigenous hill grass swards of different botanical and morphological composition were studied in relation to the seasonal cycle of herbage growth, through measurements of ingestive behaviour, herbage intake, diet composition and diet digestibility.

To test the validity of the assumption that oesophageal-fistulated and non-fistulated animals selected the same diet, a small experiment was carried out, in which the botanical composition of the faeces was found not to differ significantly between the two groups.

It was found that on sown pastures with a high herbage mass and highly accessible leaf, herbage intakes estimated from measurements of intake per bite and total daily bites were very high over short periods, but that herbage intake declined as a result of a reduction in intake per bite. It was postulated that the reduction in intake per bite was under an internal control, rather than a result of a response to changing sward conditions. The cattle grazed less selectively than the sheep with the result that the swards grazed by cattle were more evenly grazed than those grazed by sheep.

Cattle rejected a herbage fouled by their own species to a greater extent than did sheep. The conclusion was drawn that under mixed grazing a greater proportion of the herbage would be available to the sheep giving them an advantage over the cattle.

On the indigenous swards the cattle and sheep selected diets of similar OMD except in the spring and autumn on short swards containing a high proportion of dead herbage, where the sheep obtained diets between 5 and 12 units of digestibility higher than those of the cattle. Intake per bite was found to be the major determinant of daily herbage intake in both species, and was influenced primarily by sward height. Where intake per bite declined, due to declining sward height, rate of biting increased. Increases in grazing time occurred where intakes per bite were particularly low, but this was not a consistent response. The cattle responded to increases in the density of the sward by increasing rate of biting; the sheep increased grazing time. Very low intakes per bite in the early spring on short swards where the digestibility of the diet selected was low led to digestible organic matter intakes by the cattle that were only barely adequate for maintenance.

Cattle consistently ate higher proportions of grass flower stems and Juncus whilst the sheep consistently ate higher proportions of dicots. To obtain these diets the cattle grazed the surface horizons whilst the sheep grazed the base of the sward. On short swards in the spring the cattle were unable to avoid eating a higher proportion of dead herbage than the sheep.

The cattle and sheep altered their ingestive behaviour in a consistent manner across the range of swards. Changes in diet selection varied to a greater extent within season than within swards. The selective ability of the sheep, particularly when herbage quality was poor, allowed them to maintain the nutrient concentration of their diets. The cattle maximised nutrient intake, particularly in the summer months. The different grazing strategies of the cattle and sheep enabled them to be complementary rather than competitive grazers in the summer months.

I hereby declare that this thesis has been composed by myself, and except where otherwise stated, the work contained herein is my own.

T. David A. Forbes

January 1982.

CONTENTS

ACKNOWLEDGEMENTS

I wish to thank the Director, Mr. J. Eadie, and his predecessor Professor J.M.M. Cunningham, for permission to undertake this study and for providing facilities at the Hill Farming Research Organisation, Dr. J. Hodgson, my supervisor at H.F.R.O., for his continual advice, guidance and encouragement, and Dr. C. Hinks, my supervisor at Edinburgh University, for his helpful criticism of the manuscript.

The main experiment (Experiment 3) described in this thesis was carried out as an integral part of an inter-departmental study planned by Dr. J. Hodgson, Miss S.A. Grant and Mr. R.H. Armstrong. In the main study, responsibility for organising sward measurements rested with Mr. D.E. Suckling, for herbage intake measurements with Mr. R.H. Armstrong, and for analysis of diet composition with Miss S.A. Grant. I wish to thank these individuals for their help in planning the related animal behaviour studies, and for allowing the use of their data.

In addition, I wish to thank the following for their assistance and cooperation during the course of the study:

Mr. R. Thompson, in particular, and Miss H. Smith for help and advice with the statistical analyses.

Mr. M.M. Beattie for his unstinting help during the experimental work. Mr. R.H. Armstrong for help and advice in the field, together with Messrs. T.G. Common, R.A. Hetherington, W.G. Souter and J. Smith.

Mr. D.E. Suckling, Miss L. Torvell, Miss S. Sharrock, Miss C. Williams and Miss S.A. Grant for carrying out the greater part of the botanical analyses. Miss S.A. Grant and Miss L. Torvell for their part in the analysis of extrusa samples.

Dr. J.A. Rogers and Mrs. A.M. Spence for writing computer programs, and Mr. W. Watson for the use of his graph-plotting program.

Mr. D.R. Campbell and Mr. C.C. Evans and their staff for chemical analyses.

Mr. I.R. Pitkethly for preparing the photographs.

Mrs. E.B.H. Reid for typing the greater part of the manuscript, and Miss J.P. Hall for typing other parts of the text.

Dr. J.M. Bircham and Mr. J.C. Arosteguy, my contemporaries, for many stimulating discussions.

The Agricultural Research Council for providing a post-graduate studentship for the first two years of the study.

Finally, I wish to thank my wife, Gay, without whose financial, physical and mental support this thesis could not have been completed.

GLOSSARY

The following abbreviations of statistical conventions, technical terms and sward names are used throughout this thesis.

Statistical conventions	Abbreviation
Not significant	NS
Significant at the 5% level of probability	*
Significant at the 1% level of probability	**
Significant at the 0.1% level of probability	***
Standard error	SE
Standard error of a difference	SED
Coefficient of variation	CV
Confidence limits at P = 0.95	CL (0.95)
Proportion of variation accounted for by regression	r^2
Residual standard deviation	RSD

Technical terms

Dry matter	DM
Organic matter	OM
Apparent digestibility of organic matter	OMD
Digestible organic matter	DOM
Live weight	LW
Herbage organic matter intake per unit live weight	HOMILW
Principal component	PC

Sward identifiers

Ryegrass	May - June	1978	R1
Ryegrass	July	1979	R2
Nardus	June	1978	N1
Nardus	October	1978	N2
Nardus	May	1979	N3
Nardus	October	1979	N4
Agrostis-Festuca	July	1978	A1
Agrostis-Festuca	October	1978	A2
Agrostis-Festuca	May	1979	A3
Agrostis-Festuca	September	1979	A4
Molinia	June	1979	M1
Molinia	August	1979	M2
Molinia	July	1980	M3
Molinia	September	1980	M4

INTRODUCTION

Considerable progress has been made in the development of management practices which overcome the inherent limitations to animal production in traditional systems of hill farming (HFRO 1979). Foremost amongst these is the introduction of grazing control to ensure the provision of vegetation of good nutritive value at critical stages in the annual production cycle of hill sheep (Eadie, Armstrong and Maxwell, 1979; Eadie, Maxwell and Currie, 1979). However the evidence on which recommended systems of management are based is restricted to a limited range of vegetation types and to grazing sheep (Eadie, 1970; Eadie, Armstrong and Maxwell, 1973; Eadie, Maxwell, Kerr and Currie, 1973). Eadie (1981), in a review of the available evidence, concluded that in order to develop management strategies appropriate to the wide range of conditions found on hill farms, a more detailed understanding is required of the grazing behaviour and nutrient intake of cattle and sheep grazing a range of hill vegetation types.

Studies by Allden and Whittaker (1970), Stobbs and co-workers (Chacon, Stobbs and Dale, 1978), and Hodgson and co-workers (Hodgson,1981), have examined the influence of the structure of the sward on the ingestive behaviour of grazing animals, but there are few comparative studies on the responses of cattle and sheep to changes in the morphological and botanical composition of the vegetation, (Dudzinski and Arnold, 1973; Langlands and Sanson, 1976; Jamieson and Hodgson, 1979b; Hodgson, 1981). Studies by Arnold (1960a), Arnold, McManus, Bush and Ball (1964), and Arnold, Ball, McManus and Bush (1966) using sheep showed the importance of selective grazing on the diets obtained by grazing animals. Other studies on cattle (Stobbs, 1973 a & b, 1975; Chacon and Stobbs, 1976; Chacon, Stobbs and Dale, 1978; Hendrickson and Minson, 1980) showed that herbage intake could be influenced by changes in sward structure reducing the rate at which selected components were ingested. These studies were all carried out on sown swards though covering a wide range of sward conditions. There is, however, little quantitative information on the responses of animals to changes in sward conditions on indigenous vegetation.

In the project which forms the basis of this thesis the main objectives were to compare the responses of cattle and sheep in relation to the seasonal cycle of variation in the physical and nutritional characteristics of a representative range of hill and upland grass and grass-heath communities and to determine the relationships between sward characteristics, ingestive behaviour, diet selection and nutrient intake. These studies were necessarily conducted on a relatively large scale. They were preceded by detailed preliminary studies on sown swards to examine the responses in the ingestive behaviour of cattle and sheep to differences in sward structure under controlled conditions, and to examine the influence of dung in the sward upon patterns of grazing behaviour and herbage utilisation in the two species.

LITERATURE REVIEW

Introduction

The bulk of feed eaten by livestock world-wide is provided by grasslands and systems based on grazing remain the cheapest form of animal production (Morley, 1981). The level of production (meat, milk, wool etc.) from grazing animals is largely determined by the quantity of feed consumed (Blaxter, 1964; Raymond, 1969), and the factors influencing feed intake of grazing animals can be divided into four groups involving animal, sward, environmental and managerial effects (Hodgson, 1977). In this literature review the controls of herbage intake of grazing animals and the effects of sward conditions on herbage intake as mediated by ingestive behaviours are discussed first, and the process of diet selection by grazing animals is then considered. It must, however, be borne in mind that managerial decisions can markedly affect, directly or indirectly, both sward and animal variables and their interactions.

Section I Herbage intake in grazing animals

The herbage intake of grazing ruminants is controlled largely by the effects of diet composition, principally diet digestibility, on the rate of disappearance of material from the reticulo-rumen and the effects of sward structure on ingestive behaviour (Freer, 1981). These two effects correspond respectively to the intrinsic and extrinsic factors proposed by Raymond (1969), and they will be discussed in detail in the following sections. It is beyond the scope of this review to discuss the role of hormones and metabolites in controlling intake, but the subject has been reviewed recently by Baile (1975), Forbes (1980) and Freer (1981), and there is general agreement that in the long term the energy balance of the animal determines the level of intake though there is not complete agreement as to how the regulatory mechanisms function.

The effects of diet composition on herbage intake

Though many of the studies discussed were carried out on animals fed indoors, it is assumed, like Arnold (1970), that the principles hold true equally for grazing animals. It is apparent that the rate of herbage intake is limited by the rate at which the feed is digested in the reticulo-rumen, and passes out through the omasum (Campling, 1970; Bines, 1971). The rate at which herbage is digested varies with animal species (Playne, 1978), though usually differences are small except when feeds of high fibre content are involved. The digestibility of plant parts varies, leaves being more digestible than stems and immature parts being more digestible than mature parts, and there are also differences in digestibility between plant species (Terry and Tilley, 1964; Raymond, 1969; Hacker and Minson, 1981; Ulyatt, 1981). The digestibility of herbage depends on the extent to which the cellulose and hemi-cellulose fractions are broken down by the microbial flora of the reticulo-rumen, and highly fibrous material is broken down relatively slowly. Furthermore, the rate of digestion depends on an adequate supply to the microbial flora of essential nutrients such as nitrogen (Campling, Freer and Balch, 1962), and sulphur (Rees, Minson and Smith, 1974).

Many early studies showed that there was a positive linear relationship between intake and diet digestibility up to levels of 0.67-0.75 in both housed and grazing animals (Blaxter, Wainman and Wilson, 1961; Blaxter and Wilson, 1962; Hutton, 1962; Corbett, Langlands and Reid, 1963; Conrad, Pratt and Hibbs, 1964). Above these levels some authors found a curvilinear relationship (Blaxter, and Wilson, 1962; Corbett et al, 1963), whilst others, (Hutton, 1962;

Conrad et al, 1964) found no relationship between intake and digestibility at levels above 0.67-0.75. As a result it was thought that above these levels physical effects ceased to control herbage intake and metabolic controls became important (Conrad et al, 1964; Corbett, 1969). However more recent studies have found no significant deviation from linearity of regressions of intake on digestibility up to levels of 0.80-0.82 under grazing conditions (Hodgson, 1968; Jamieson, 1975; Hodgson, Rodriguez Capriles and Fenlon, 1977). The differences between the early and later studies can be ascribed to differences in the class of stock used, with the early studies being carried out on mature animals whilst the later studies have all used young growing animals with higher nutrient demands. Hodgson (1977) concludes that under grazing conditions the herbage intake of productive animals is seldom affected by metabolic limits.

Since the rate at which food residues pass out of the reticulo-rumen is controlled by the rate at which feed particles are digested intake must also be controlled by the capacity of the reticulo-rumen. It has been shown (Campling, 1970) that both cattle and sheep eat to a constant level of rumen fill, but this does not appear to hold true for all ruminants. Milne (1980) has shown that the weight of rumen contents and the capacity of the rumen of red deer increases between the winter and the spring, suggesting that red deer at least have the ability to raise and lower the threshold levels for the rumen-wall stretch receptors. Egan (1970) has demonstrated that rumen fill in sheep does not operate as a mechanism controlling intake at a preset level, but rather is variable and is sensitive to a number of factors, including the protein nutrition of the animal.

The effects of sward conditions on herbage intake

The effects of sward conditions on herbage intake are mediated by ingestive behaviour variables which change in response to changing sward conditions. These ingestive behaviour variables are intake per bite, rate of biting and grazing time, and it is customary to equate the effects of the ingestive behaviours on intake in the following equation.

Herbage intake = Intake per bite x Rate of biting x Grazing time

Intake per bite is considered to be the dominant influence on herbage intake with rate of biting and grazing time acting as compensatory behaviours (Hodgson and Milne, 1978). The next three sub-sections discuss the role of each behaviour in relation to herbage intake and its response to changes in the sward.

Intake per bite: Though the importance of intake per bite has been recognised for many years, it is only relatively recently that attempts have been made to measure it in grazing animals. Three methods of measuring intake per bite have been published. The first (Allden and Whittaker, 1970) involves calculating intake per bite from estimates of the rate of biting and herbage intake during hourly measurement periods. Values of 20-400 mg DM per bite were recorded in this manner in lambs grazing Wimmera ryegrass (Allden and Whittaker, 1970). The second technique involves recording the number of bites taken whilst oesophageal-fistulated animals collect known quantities of extrusa (Stobbs, 1973a&b; Jamieson, 1975). This technique is now widely used in grazing studies and values of intake per bite have been found to range from 70 mg OM to over 590 mg OM per bite in cattle grazing a range of tropical swards (Stobbs, 1973a &b). These values when converted to mg OM/kg LW (assuming Stobbs' Jersey cows weighed around 400 kg LW) are substantially lower than those found by Jamieson (1975) for calves grazing a temperate ryegrass sward, the values being respectively 0.32-0.97 mg OM/kg LW and 0.94-3.04 mg OM/kg LW. The third technique involves the indirect calculation of intake per bite from measurements of herbage intake and either rate of biting and grazing time or total daily bites measured directly. (Jamieson, 1975; Chacon, Stobbs and Sandland, 1976). This method depends on the accuracy of the estimates of the three parameters and was found by Jamieson to under-estimate intake per bite due to over-estimation of rate of biting.

The importance of intake per bite in relation to the herbage intake of grazing animals has been stressed by Stobbs (1973a) who calculated that cattle weighing 400 kg LW grazing tropical swards might have restricted intakes if the mean intake per bite fell below 0.3 g OM. Lighter animals would have restricted intakes at lower intakes per bite and heavier animals restricted intakes at higher intakes per bite assuming intakes of the same proportion of body weight.

Intake per bite has been shown to increase linearly with increasing sward height in both cattle and sheep grazing both temperate and tropical grass swards (Allden and Whittaker, 1970; Chacon and Stobbs, 1976; Chacon, Stobbs and Dale, 1978; Hodgson, 1981). Stobbs (1973a&b), however, found that on some tall tropical grass swards the relationship between intake per bite and sward height was negative rather than positive and he (Stobbs, 1975) ascribed this to the low density of leaf at the sward surface. In fact in tropical grass swards intake per bite appears more closely related to leaf density at the sward surface or to the leaf/stem ratio, than to sward height (Stobbs, 1973a&b; Stobbs, 1975; Chacon and Stobbs, 1976), and a similar conclusion was drawn by Hendricksen and Minson (1980) from the results of cattle grazing on tropical legumes. The influence of intake per bite on herbage intake is illustrated by the results of Hendricksen and Minson (1980) who found that a reduction in intake per bite from 410 mg OM to 90 mg OM over a 12 day period resulted in a linear reduction in herbage intake of over 925 g OM/day. In this study the cattle concentrated their grazing on the green leaf fraction of the sward and by the end of the experiment were probably at the stage of selecting individual leaves. The evidence of Stobbs (1975) suggests that the cattle in his experiment were virtually grazing individual leaves. Hodgson and Milne (1978) have reported a positive linear relationship between intake per bite of sheep and herbage mass. They determined intake per bite by recording the number of bites taken to collect a known weight of extrusa and found intakes per bite per kg LW to range from 835 mg DM to 1457 mg DM when the animals grazed predominantly ryegrass swards ranging in mass from 1200 kg/ha to 3000 kg/ha. Subsequently Hodgson (1981) suggested that the bite volume must have declined markedly as the swards were grazed down since the density of herbage increased towards the bottom of the swards. Recent evidence (Barthram, 1980) has shown that, in sheep at least, the depth of the sward horizon in which grazing takes place declines as the horizons containing dead leaf and vegetative stem are approached. A reduction in the depth of the bite is likely to reduce intake per bite since an increase in the width of the bite is limited by the width of the mouthparts. There is no evidence available to suggest what the theoretical maximum bite volume might be. In any circumstances where animals are grazing selectively the intake per bite is likely to be less than maximal, and thus measurements of width across incisors or buccal cavity volume are likely to be unreliable indicators of intake per bite.

Rate of biting: The measurement of rate of biting as an indicator of sward conditions has been carried out for at least 40 years (Johnstone-Wallace and Kennedy, 1944), but it is only recently that rate of biting has been used as a parameter which can be used, together with grazing time and intake per bite, to determine herbage intake. The measurement of rate of biting may be manual or automatic but both techniques demand an adequate definition of a "bite". Manual recording can only be done on the basis of individual 'events' which may or may not be recorded against a time base whilst automatic recording can provide a continuously variable record, usually against a time base, or a series of 'event' records.

Jamieson and Hodgson (1979a) describe a technique for manual bite rate recording whereby the time taken by animals to make 20 bites is recorded by stopwatch, and then biting rates are calculated as bites per minute. In this technique each bite is characterised by a short, sharp upward jerk of the animal's head, usually, and particularly in cattle, accompanied by a distinctly audible noise as the herbage is torn away. Records are discarded if the animal raises its head before 20 bites are completed. Allden and Whittaker (1970) recorded rates of biting by direct observation over 3-minute periods, but they do not characterise the bite. Jamieson (1975) in developing the 20-bite technique compared it with records made over 2 minutes, and found that the 20-bite technique gave rates of biting 16.4% higher than the rate of biting measured over 2 minutes, because the latter technique takes into account more of the normal and characteristic movements animals make during grazing, such as lifting the head while chewing large mouthfuls, walking between bites etc. Differences between the two techniques were greatest in the morning, though no explanation for such a difference is given.

It is important that records of biting are made on several occasions throughout the day, and over several days, to avoid both diurnal effects and between-day differences due, for example, to variations in the weather. Hodgson (in press) describes the basic requirements of automatic behaviour recorders in relation to rate of biting recording and states the necessity for acceptable criteria to define biting activity. Automatic recorders of biting activity for grazing animals have been described by Canaway, Raymond and Taylor (1955), Stobbs and Cowper (1972) and Chambers, Hodgson and Milne (1981).

Hancock (1954) and Stobbs (1974) found that rate of biting declined linearly over the course of an individual grazing period. Hodgson (1969) reported no difference in rate of biting between grazing periods, but more recently evidence has been put forward that rate of biting may fluctuate diurnally, being faster in the morning and evening than at midday (Rodrigeuz Capriles, 1973; Elizabeth MacPherson, personal communication).

Actual rates of biting for cattle and sheep have been shown to vary quite markedly. Stobbs (1974) found that cattle bite rates varied from 45 to 80 bites per minute when grazing various tropical swards, whilst Hodgson and Jamieson (1981) reported bite rates for lactating cows to range from 19.7 to 62.3 bites per minute while grazing temperate ryegrass swards. Sheep have been reported to take as few as 18 bites per minute (Allden and Whittaker, 1970) and as many as 120 bites per minute (J. Wadsworth, personal communication). There are few records of bite rates of cattle and sheep grazed together, but what little evidence there is suggests that cattle generally have faster rates of biting than sheep (Jamieson, 1975). Weaned calves grazing with lactating cows were found to have bite rates intermediate in range to those of the adults (Hodgson and Jamieson, 1981) though Wadsworth (personal communication) found that lambs had slower rates of biting than ewes.

Rate of biting by sheep grazing Wimmera ryegrass was observed to increase as sward height decreased until an apparent maximum of 73 bites per minute was reached at a sward height of 5 cm, at which point rate of biting declined sharply (Allden and Whittaker, 1970). Hodgson (1981), however, found no relationship between rate of biting and sward height in either calves or lambs set-stocked on a temperate ryegrass sward, whilst in one experiment strip-grazed calves were found to reduce rate of biting with declining sward height. Hodgson and Jamieson (1981) have suggested that the low rates of biting found in lactating cattle (19.7 bites per minute) were due to the very tall swards, (extended heights between 79 and 88 cm). J. Wadsworth (personal communication) found that sheep and lamb bite rates declined curvilinearly rather than rectilinearly, though the trend followed that found by Allden and Whittaker (1970) even though the range of sward heights were not comparable. Rates of biting have also been found to increase with declining herbage mass (Hodgson and Wilkinson, 1968; Chacon and Stobbs, 1976; Jamieson and Hodgson, 1979a&b). Chacon and Stobbs (1976) found that rate of biting was negatively correlated with the proportion of leaf and the leaf/stem ratio of tropical grass swards.

Grazing time: The measurement of grazing time, as well as rate of biting, goes back for many years (Johnstone-Wallace and Kennedy, 1944). Measurement of grazing time can be carried out manually or automatically though due to the time involved in the collection of data and the simplicity of the simplest automatic recorders most grazing time measurements are now carried out automatically. Manual methods generally involve recording the activity of the animals at 5- or 10-minute intervals over a period of 24 hours. Due to the labour involved recording periods are seldom longer than 24 hours. The most commonly used automatic recorder is the Kienzle vibracorder (Allden, 1962; Stobbs, 1970), though some electronic apparatus has been used (Canaway, Raymond and Taylor, 1955; Chambers, Hodgson and Milne, 1981). Continuous records can be made for up to 8 days in the case of the Kienzle vibracorders.

Grazing time has been examined from two view-points: in the first, grazing time is examined in the context of the behaviour of grazing animals as a whole, whilst in the second grazing time is examined as a variable in controlling herbage intake. Studies on grazing time as a component of grazing behaviour have shown that in general sheep and cattle spend about one third of the day actually grazing, though a range of values has been found ranging, for cattle, from 264 minutes per day (Hancock, 1954) to 816 minutes per day (Stobbs, 1970) and, for sheep, from 420 minutes per day (Arnold, 1960b) to 810 minutes per day (J. Wadsworth, personal communication), depending on class of animal and sward conditions. Few studies have compared the grazing times of cattle and sheep grazing together, but it appears that sheep graze for one to two hours longer than cattle (Hughes and Reid, 1951; Lofgreen, Mayer and Hull, 1957; Jamieson and Hodgson, 1979b). Differences in grazing time have been reported between breeds in cows (Brumby, 1959) and in sheep (Arnold and Dudzinski, 1967a) and between animals of differing physiological state (Hancock, 1952; Brumby, 1959; Arnold and Dudzinski, 1967a; Mugerwa, Christensen and Ochetim, 1973; Stobbs and Hutton, 1974), with lactating cattle grazing for longer than dry animals. However, Arnold (1962) found that grazing time was not increased by pregnancy or lactation in ewes though seasonal effects may have confounded the results. Positive relationships between grazing time and milk yield have been described by workers in the tropics (Stobbs, 1970; Cowan, 1975), but not in temperate areas (Johnstone-Wallace and Kennedy, 1944; Hancock, 1950). Young animals appear to graze for longer than mature animals (Roy, Shillam and Palmer, 1955; Hodgson and Wilkinson, 1967). Jamieson and Hodgson (1979b) reported grazing times for calves and lambs that were higher than previously reported results for cattle and sheep in Britain (Hughes and Reid, 1951; Le Du, Baker and Barker, 1976; Le Du, Combellas, Hodgson and Baker, 1979) though these long grazing times may be more a reflection of sward conditions than inherent differences between young and old animals.

Most studies on grazing time have included details of grazing periodicity. There is more evidence available for cattle than for sheep but generally animals appear to graze on four or five occasions during the day (Atkeson, Shaw and Cave, 1942; Castle, Foot and Halley, 1950; Hughes and Reid, 1951; Hancock, 1953; Tayler, 1953; Chambers, 1959; Gary, Sherrit and Hale, 1970). Arnold (1962) recorded that wether sheep had an average of 7.5 grazing periods per day. Whatever the distribution of grazing periods during the day the major periods in terms of length of grazing occur at dawn, mid-morning, mid-afternoon and dusk (Atkeson, Shaw and Cave, 1942; Castle, Foot and Halley, 1950; Hancock, 1950; Hughes and Reid, 1951; Ellis and Travis, 1974; Cowan, 1975). Night grazing in temperate areas makes up only a small proportion of total grazing time (Hancock, 1950; Tayler, 1953; Waite, McDonald and Holmes, 1951; Jamieson and Hodgson, 1979b), though it increases with decreasing day length (Tayler, 1953; Hancock, 1953). In tropical areas, however, night grazing can contribute significantly to the total grazing time (Cowan, 1975), particularly for high-yielding dairy cows (Stobbs, 1970).

A very much smaller number of studies have examined grazing time as a variable involved in the determination of herbage intake. They include studies on cattle grazing tropical swards in Australia (Stobbs, 1970, 1974, 1975, 1977; Stobbs and Hutton, 1974; Chacon and Stobbs, 1976; Chacon, Stobbs and Sandland, 1976; Chacon, Stobbs and Dale, 1978), on sheep in Australia (Arnold, 1960b; Allden, 1962; Arnold and Dudzinski, 1966; Allden and Whittaker, 1970; Arnold and Birrel, 1977), and on cattle and sheep in the United Kingdom (Hodgson and Wilkinson, 1967; Jamieson, 1975; Jamieson and Hodgson, 1979a&b; Le Du, Combellas, Hodgson and Baker, 1979; Hodgson and Jamieson, 1981). In general there is a negative correlation between time spent grazing and sward height or herbage mass. Allden and Whittaker (1970) found that grazing time increased rapidly with a decline in herbage mass below 1000 kg DM/ha. Chacon and Stobbs (1976) found poor correlations between grazing time and sward characteristics when a tropical grass sward was grazed down over a fortnight. However, there was evidence that grazing time was negatively correlated with herbage mass in the first half of the fortnight but then became positively correlated in the second half. Jamieson and Hodgson (1979b) reported significant negative relationships between grazing time and green herbage mass for both calves and lambs. J. Wadsworth (personal communication) found a significant quadratic relationship between grazing time and herbage mass in sheep with short grazing times at both low and high herbage masses. He found a similar quadratic relationship between grazing time and sward height, whilst the relationship between grazing time and sward density was positive but non-significant. A similar quadratic function was found by Hendricksen and Minson (1980) for the regression of grazing time by cattle on the yield of leaf of a tropical legume.

Relationships between ingestive behaviour variables and their combined influence on herbage intake

The ingestive behaviour variables reviewed above do not act on intake in isolation, but rather, their individual responses to changing sward conditions are modified by the extent of the change of the other variables. It does, however, appear that intake per bite has a greater influence on daily herbage intake than either rate of biting or grazing time. Rate of biting and grazing time may be considered as 'compensatory' variates. Thus where intake per bite is declining due to a reduction in herbage mass or sward height, rate of biting and/or grazing time are generally found to increase. It appears, however, that there may be limitations to the amount of compensation that can occur, especially in certain circumstances. Jamieson and Hodgson (1979a) along with Combellas and Hodgson (1979) and Le Du et al (1979) working with strip-grazed calves and strip-grazed dairy cows found that at low herbage allowances grazing time was reduced which, combined with low intakes per bite, resulted in reduced herbage intakes. Jamieson and Hodgson (1979a) attributed this decline in grazing time to a conditioning effect of strip-grazing on the calves.

Allden and Whittaker (1970) showed that as rate of intake (intake per bite x rate of biting) declined with declining herbage mass so their sheep began to increase grazing time in compensation; at very low levels of herbage mass, however, compensation becomes progressively more incomplete. Hendricksen and Minson (1980) showed that as intake per bite declined in parallel with the yield of green leaf their cattle increased rates of biting and grazing time, but not sufficiently to compensate for the increasingly smaller intakes per bite. Grazing time was reduced at green leaf yields below 1200 kg/ha and thus intakes fell even faster. At some stage during grazing on certain swards animals must be faced with the decision of whether to continue grazing for long periods at low rates of intake. Under conditions of severely limited food intake, whether this shortage is due to a physical absence of feed or a lack of desire on the animals part to graze unappetizing herbage, it may be advantageous for animals to reduce energy expenditure by reducing grazing activity. Young and Corbett (1972) reported maintenance requirements of grazing sheep to be 60-70% greater than those for housed sheep of similar liveweight, and that animals that had been on good pasture when put on poor pasture reduced their daily energy expenditure by about 70kJ/kg $LW^{0.75}$. Though rate of biting declines at low herbage mass and low sward height it is not possible to distinquish between effects of fatigue or effects of diet selection, both of which might reduce rate of biting.

Changes in sward conditions lead to different responses in ingestive behaviour, and thus it can be difficult to obtain a clear picture of the overall change in herbage intake in response to changes in sward conditions. Many workers have found that the relationship between herbage intake and herbage mass is asymptotic, although the actual herbage mass below which herbage intake is depressed varies between experiments (Johnstone-Wallace and Kennedy, 1944; Tayler, 1966; Hodgson, Tayler and Lonsdale, 1971; Hodgson, 1977). However, Hodgson and Milne (1978) and Jamieson and Hodgson (1979b) found no evidence that the relationship between intake and herbage mass deviated from linearity, even at herbage masses over 3000 kg/ha. Hodgson and Milne (1978) suggested that other sward variables such as sward height, leaf/stem ratio or herbage density may modify the overall relationship between intake and herbage mass, thus leading to the variation in the critical mass that has been found. Jamieson and Hodgson (1979b) suggested that the lack of an asymptote reflected either the higher potential nutrient intakes or the greater sensitivity to sward conditions of their young cattle and sheep. Though Jamieson and Hodgson (1979b) reject the second alternative as being unlikely, Allden and Whittaker (1970) found that lambs were better at maintaining intake on very short swards than older animals, and Hodgson and Jamieson (1981) suggest that calves that are experienced grazers may be particularly sensitive to variations in herbage mass.

Sward height has also been found to be an important influence on herbage intake. When comparing results obtained by different workers allowance must be made for differences in measurement techniques. Sward height has been measured in a variety of ways, which have been reviewed recently (Rhodes, 1981). Hodgson (1981) suggested that in temperate swards the surface height of the sward determines rate of herbage intake to a greater extent than the density of herbage or proportion of live material at the surface. This is not the case with tropical swards where tall swards generally have low surface densities and thus intake per bite is low and hence rate of intake is depressed (Stobbs, 1973a&b). Allden and Whittaker (1970) found in one experiment that sward height was closely associated with rate of intake and that herbage mass and intake were scarcely related. The influence of herbage density on intake, either in the sward as a whole or in individual sward horizons, has been described by Spedding and Large (1957), Chacon and Stobbs (1976), Chacon, Stobbs and Dale (1978), Hodgson (1981) and Wade and Le Du (1981). Swards of low density reduce the ease of prehension of the herbage and thus rate of intake declines.

Environmental influences on herbage intake

Isolating the effects of environment on herbage intake or on ingestive behaviour variables is extremely difficult, but there is some evidence that certain environmental factors do influence herbage intake. Probably the most important effect is that of season, which acts through day-length. It has been shown that domestic ruminants show an appetite cycle which is stimulated by changes in day-length similar to, though less marked than, the appetite cycle found in wild deer (Kay, 1979). Unlike season, the effects of weather are likely to affect herbage intake only indirectly via the ingestive behaviour variables. Munro (1962) found that sheep sought shelter only when the wind speed exceeded 24 m.p.h.. Rain has been found to have little effect on grazing behaviour (Waite et al, 1951; Hancock, 1952; Rutter, 1968) though animals will stop grazing for short periods in very heavy rain. There is no information on relationships between the weather and rate of biting or intake per bite. Temperature has not been found to influence grazing behaviour in temperate climates even at day-time temperatures in excess of 30°C (Gary et al, 1970). In hot climates there is often a reduction in day-time grazing but with a compensatory increase in night grazing (Payne, 1966; Cowan, 1975). Holder (1960) found no change in the grazing behaviour of cattle on especially hot days.

Conclusions

Intake of herbage may be restricted in grazing animals if the grazing behaviour variates cannot compensate for changes in sward conditions. Situations where compensation for reduced rate of intake is not complete have been described on both temperate (Allden and Whittaker, 1970), and tropical swards (Chacon and Stobbs, 1976). In general herbage intake is determined by sward height or mass via the ingestive mechanisms which allow the animals to compensate for changes in sward conditions. In grazing animals intake is seldom controlled by metabolic controls since the limitations are either behavioural or physical. The number of factors affecting herbage intake is considerable and the use of powerful computing methods such as principal component analysis or other multivariate techniques, as suggested by Dudzinski and Arnold (1973) and Wade and Le Du (1981), are called for before a much greater understanding of the grazing system is obtained.

Section II Diet selection by grazing animals

Definitions

Before reviewing the literature dealing with the selection by animals of plant communities, or plants and/or parts of plants within the sward, it is necessary to clarify some of the terminology used in describing the processes of diet selection. For this purpose heavy reliance has been placed on Hodgson's (1979) nomenclature and definitions in grazing studies. Availability of herbage has been used and is still frequently used to describe the total herbage mass of the sward, as well as to describe the ease with which the herbage may be grazed. Hodgson (1979) recommends the use of herbage mass in the first instance and ease of prehension in the second. Ease of prehension is determined by the size and strength of the herbage components and their position within the sward canopy, and is thus a qualitative term, quantifiable only in terms of its effect on intake per bite and rate of biting. Preference and palatability have also been used interchangeably in the literature with consequent confusion. Marten (1969) reviewed various definitions of palatability such as that of Stapledon (1947),

..."an appeal sufficient to hold animals to the grazing of one species for days or even weeks on end, and a standard of tastiness that will attract animals to particular plants when the scope for selection is comparatively wide."

and Tribe and Gordon's (1950) definition,

"The adjective palatable may in fact be taken as the nutritional synonym of the word 'attractive', and the palatability of a food is the sum of the factors which operate to determine whether, and to what degree, the food is attractive to an animal."

Marten (1969) also mentions the definitions of Jones (1952), Stoddart and Smith (1955), Joblin (1962) and Heady (1964). Stoddart and Smith (1955), Heady (1964) and Petrides (1975) all suggested that a distinction could and should be drawn between palatability and preference. Hodgson (1979) suggested that palatability should only be used in those rare cases where the strict dictionary definition of palatability meaning, 'pleasant to taste' (Concise Oxford Dictionary, 1976), can be applied. Marten (1969) introduced a 'conceptual definition of relative forage palatability' which has greater affinities with definitions of preference than the above dictionary definition of palatability.

In this review the definitions given by Hodgson (1979) for herbage mass and ease of prehension will be used; palatability will not be used except as defined by the dictionary. Preference will be used to describe situations where animals respond to swards or to components within swards in a discriminating manner. The term selection has already been used in the heading of this section. It is used here as a function of preference, to describe the choice made between one plant community and another, or the choice and subsequent removal by grazing of some component of the sward rather than another. In essence selection is preference modified by opportunity. Opportunity arises from a combination of sward and animal factors that together determine the accessibility of the sward and its components to the grazing animal. These factors are discussed later when dealing with the influence of sward structure and animal mouthpart structure on diet selection.

Dietary preferences

Since grazing animals select herbage on the basis of preference modified by opportunity any review of diet selection should examine the evidence for dietary preferences. Preference is unlikely to be successfully determined in grazing trials because the structure of the vegetation may itself limit the animals access to certain components, and because the relative proportions of sward components change immediately grazing starts, leading to a situation where complete freedom of choice, a prerequisite for such trials, is absent.

Animal factors influencing preference: Kare (1969) reported that different animal species live in worlds differing in taste and, presumably, other senses which may or may not overlap. Goatcher and Church (1970a&b) made extensive comparisons between goats, sheep and cattle on the basis of the lowest concentration of a chemical solution to be discriminated, and found that sensitivity to sweet, salt, sour and bitter was as follows:-

	Lowest sensitivity						Highest sensitivity
Sweet	Cattle	>	Normal goats	>	Pygmy goats	>	Sheep
Salt	Cattle	>	Pygmy goats	>	Normal goats	>	Sheep
Sour	Cattle	>	Pygmy goats	=	Sheep	>	normal goats
Bitter	Pygmy goats	=	Normal goats	>	Sheep	>	Cattle

Goatcher and Church (1970a&b) also found within-species differences in the rankings of initial discrimination to sweet, salt, sour and bitter. They related these findings to the dietary preferences of the animals, suggesting that the tolerance of goats and sheep for bitterness reflects the greater browse component of their diets. Arnold and Hill (1972) have reviewed the responses of ruminants to the taste and smell of chemical solutions and suggest that studies on animal responses to tastes and smells are often of little value in understanding preference determination by grazing animals. Many of the chemicals used such as quinine compounds or acetic acid are rarely found in plants in the forms tested; furthermore the taste/ smell sensation is not a simple choice but involves different combinations and concentrations of the four major taste sensations. Arnold and Hill (1972) postulate that with lengthening exposure to a taste sensation, concentrations that lead to rejection will be reduced. Earlier Tribe (1949) had suggested that since adaptation to odours occurred rapidly (20-40 minutes) smell could only be of supplementary importance in influencing preference. However Arnold and Hill (1972) reported that sheep appeared to take up to 24 hours to decide their response to odours. There appear to be sex differences in deer related to taste (Crawford and Church, 1971; Rice and Church, 1974) but the practical consequences of such differences are unknown. Previous experience is likely to play an important part in influencing preference (Arnold and Maller, 1977) and differences in preference are likely to be greatest when diverse experiences occur at an early age.

Individual variation in taste response is of importance to grazing animals since it widens the choice of foods available to the population. However, it is noticeable how many plant species are avoided by all members of a grazing population, indicating that certain plants may contain chemical compounds that are recognised as being unpleasant if not actually harmful by all the individuals.

The role of instinct in determining preference and selection

The evolution of grazing animals and their continued survival suggests that they have sensory responses capable of determining nutritionally adequate intakes. McClymont (1967) suggests that assuming equal physical accessibility two types of selective eating can be described. Euphagia - food selection directed towards optimal nutrition, and Hedyphagia - food selection directed towards maximising pleasant and minimising unpleasant olfactory, gustatory and other sensations. Where selection for a specific nutrient is observed this may be termed specific euphagia.

Examples of specific euphagia appear to be confined to the selection for sodium. Denton and Sabine (1961), Bell and Williams (1960) and Baldwin (1968) working with sheep, cattle and goats respectively have shown that these animals can select sodium solutions and maintain a positive sodium balance. The evidence for other elements is not so clear cut. Stewart (1953) found that cobalt-deficient sheep preferentially grazed swards top dressed with cobalt sulphate, but the animals would not eat cobalt-rich mineral licks. Similarly Gordon, Tribe and Graham (1954) found that phosphorus-deficient cattle and sheep could not be induced to eat a dicalcium-phosphate-ground limestone mixture even though phosphorus deficiency was such that osteophagia was evident. Reid and Jung (1965) found that though phosphorus-deficient sheep preferred a tall-fescue hay treated with a phosphorus fertilizer to an untreated hay, this preference remained even after treatment of the animals with a phosphorus supplement, suggesting that it was not the phosphorus alone that induced the preference. More recently Ozanne and Howes (1971) have reported preferential grazing of phosphorus-fertilized swards by sheep and suggested that this was due to a reduction in the free-phenol content of the pasture.

Generally ruminants, like nearly all other animals, appear to be hedyphagic. The addition of sugar to calf diets increased feed intake (Preston, 1958) and spraying faeces-contaminated pasture with molasses induced cattle to eat more of the initially unacceptable herbage (Marten and Donker, 1964a). There is no conclusive evidence, however, that animals can recognise the chemical composition of plants. Arnold and Hill (1972) suggested that domestication of animals may have led to a reduction in sensitivity to various stimuli as a result of the presentation of feed to the domesticated animals by man producing stimuli outside their inherent sensitivity ranges. This may explain the observation of Arnold and Hill (1972) that sheep and not kangaroos in Western Australia preferentially eat plants of certain species which contain lethal levels of monofluoroacetate. Similarly Ivins (1955) has pointed out the seeming preference of livestock in Britain for toxic plants such as Yew (Taxus baccata), and he comments ..."this cannot be regarded as an inherent desire on the part of the animal to commit suicide."

Diet selection

The process of diet selection presents the grazing animal with two separate decisions, the first involving the animals grazing strategies and the second its tactics. Ellis, Weins, Rodell and Anaway (1976) reviewed some of the concepts involved in selection strategies and tactics. Diet selection strategies, it is suggested, arise from natural selection and may consist of one or more of the following: the maximisation of energy intake (Schoener, 1971; Emlen, 1973), the maximisation of feeding time (Schoener, 1971) and the optimisation of nutrient balance (Emlen, 1973). Tactics, on the other hand, vary with animal species and environment, and their employment depends on such components as hunger, preference, and accessibility of food. For the grazing animal tactics of diet selection can occur at two levels :(1), selection for plant community and (2), selection within the sward canopy of a community.

Selection for plant community

Domesticated animals frequently do not have the opportunity to choose between alternative plant communities, particularly under intensive grazing management but, in areas where extensive grazing takes place, selection for plant community has been observed in sheep (Hunter, 1962; Weston, 1969; Griffiths, 1970), cattle (O'Donnell and Walton, 1969; Low, 1972; Low, Birk, Loudon and Low, 1973; Rosier, Beck and Wallace, 1975; Low, Dudzinski and Muller, 1981) and in many species of wild animal (Lamprey, 1963; Bell; 1969; Petersen and Casebeer, 1971; Low, Birk, Loudon and Low, 1973; Field, 1975; Marcum, 1976; Charles, McCowan and East, 1977; Breymeyer and Van Dyne, 1980; Leader-Williams, Scott and Pratt, 1981). In all areas and with all animal species selection between sites has been shown to be heavily influenced by the productivity and seasonal presence of herbage, and by apparent animal preferences. In some regions, notably the tropical grasslands, the height and density of the vegetation may prevent its use by smaller herbivores at least until it has been grazed and trampled down by larger species (Vesey-Fitzgerald, 1960; Bell, 1969).

Wild herbivores are likely to select different plant associations depending on their food requirements and their need for cover to avoid predators. In general small species have higher metabolic rates than larger species (Brody, 1945), and thus require better-quality diets (ie of higher digestibility and nutrient content) than larger animals. However, large animals have greater requirements, in absolute terms, for food. It has been shown that, in general, smaller species do in fact forage in plant associations that are able to provide such high quality diets (Bell, 1969; Jarman, 1974; Jarman and Sinclair, 1980). Larger species select plant communities apparently on the basis of sward structure rather than nutritional quality (Duncan, 1975; Sinclair, 1977). In New Zealand there is evidence that sheep concentrate their grazing on sunny slopes regardless of quantity or quality of the herbage on adjoining shaded slopes (Stevens, 1977).

Social behaviour may influence the selection of grazing areas. Work by Hunter (1962), Hunter and Davies (1963), Hunter and Milner (1963) and Griffiths (1970) on home-range behaviour in hill sheep showed that the formation of home-ranges prevented equal use of the pasture by all the animals, and that some home-ranges were superior in herbage quality to others. Animals introduced to established flocks developed their own home-ranges on areas of lower quality. Hunter and Milner (1963) noted that home-range behaviour varied seasonally, but the reduction in territorial behaviour is unlikely to greatly benefit the weaker members since the difference between the plant associations may be less because of the general decline in herbage digestibility in autumn and winter. The effects of social facilitation are such that within a group of animals activity patterns tend to be fairly uniform. Waite et al (1951) found that individuals rarely spent more than 20% of the time in activities different from the majority of the herd. O'Donnell and Walton (1969) found that no individual grazed on a plant association different to that grazed by the herd for any significant length of time. Both these findings suggest that groups of animals will tend to graze the same plant associations at the same time reducing an individuals opportunity for selection.

The ability of animals to select areas in which to graze may well be influenced by age and experience. Evidence is however scanty, though Arnold (1964), Langlands (1969) and Arnold and Maller (1977) all report differences in preference, intake or diet composition between sheep from differing backgrounds.

Selection for components within the sward

Selection within the sward can occur at two levels: firstly at the level of the individual plant and secondly within the individual plant at the level of individual leaves, stems etc. Many sown swards consist of mono-cultures where selection can only be for leaves or stems, but most swards are heterogeneous with many different species of plant with marked differences in morphology.

Selection for individual plant species differs between animal species, as has been shown in a very large number of studies, many of which have been reviewed by Breymeyer and Van Dyne (1980). In the majority of these studies, however, there is little or no information relating differences in the diets selected to differences either in the sward structure or in animal behaviour.

There is limited evidence to suggest that the distribution of individual plants within the sward influences their consumption. Harper and Sagar (1953) reported that in buttercup infested grass swards the association of preferred species amongst less preferred or rejected species reduced the consumption of the preferred plants. Wolton, Brockman and Shaw (1970) suggested that sheep preferentially selected clover from mixed grass-clover swards. Cahn and Harper (1976) have suggested that the lack of dominance of individual morphs of the white leaf mark polymorphism in Trifolium repens is due to apostatic selection of the commonest morphs by grazing sheep. Apostatic selection involves the formation of search images of the various prey forms; in this way rare forms are ignored until they become common. McNaughton (1978) suggested that preferred plant species were protected by unpalatable plant species from unselective grazers but not from selective grazers. This may be interpreted though as revealing differences in preferences rather than differences in selective ability by the animals concerned. Laycock (1978) has reviewed the literature regarding the co-evolution of livestock and poisonous plants, mainly in North America, and suggests that large herbivores have the means to detect and avoid poisonous plants under certain circumstances, but does not elaborate on the means of detection, though it is possible that aversive conditioning plays some part.

It is generally accepted that grazing animals select young, green herbage in preference to old, dead herbage (Cowlishaw and Alder, 1960; Reppert, 1960; Arnold, 1962; Talbot and Talbot, 1962; Langlands and Holmes, 1978) and leaf in preference to stem (Arnold, 1960a; Reppert, 1960; Talbot and Talbot, 1962; Van Dyne and Heady, 1965; Chacon and Stobbs, 1976; Gardener, 1980). Theron and Boysen (1964) found that the tensile strength of the leaves of various South African grasses was the most important determinant of preference. A further consequence of selecting for certain components of the sward is that the diet selected is generally of higher digestibility than the sward as a whole (Raymond, Minson and Harris, 1956; Meyer, Lofgreen and Hull, 1957; Stobbs, 1973b; Hodgson, Rodriguez Capriles and Fenlon, 1977; Langlands and Holmes, 1978). However, Hamilton, Hutchinson Annis and Donnelly (1973) found that whilst sheep did select diets higher in digestibility than the herbage on offer when green herbage mass was high; when green herbage mass was low the digestibility of the diet was lower than that of the green material in the sward. Young green herbage is usually higher in nitrogen than mature green herbage and thus the diet usually has a higher nitrogen content than the herbage on offer (Hardison, Reid, Martin and Woolfolk, 1954; Weir and Torell, 1959; Arnold, 1960b; Bredon, Torell and Marshall, 1967; Wallace, Free and Denham, 1972; Stobbs, 1973b; Langlands and Holmes, 1978; Gardener, 1980; Romero and Siebert, 1980). Since animals select young, green leaf it is not surprising that the diet is lower in fibre than the sward as a whole (Hardison et al, 1954; Weir and Torell, 1959). The diet selected is also higher in minerals (Langlands and Holmes, 1978) and again this is consistent with selection for green material as opposed to dead. Most of the above authors have noted seasonal differences in selection or avoidance of sward components, most of which appear to be related to changes in sward structure or relative changes in proportions of green and dead or leaf and stem.

Much of the selection described above is determined to a large extent by the structure of the sward. Vegetative tillers of grass carry the youngest leaves at the top and thus the surface horizons of grass swards usually have a higher digestibility than the lower horizons (Hacker and Minson, 1981). The development of reproductive material results in the formation of an upper horizon of floral parts supported by the flower stems. There are, however, considerable between and within plant species differences as to the onset of reproductive growth and thus the sward as presented to the animal consists of a mosaic of leaf and stem distributed vertically as well as horizontally.

The opportunity animals have for selection of components from within the sward depends on both the structure of the sward, the animals ability to penetrate if necessary into the sward and their ability to harvest the vegetation present. Though in general different animal species do appear to select for similar components as described above, there are differences between animal species in the relative ease with which herbage is prehended. Ease of prehension is determined by the position of the herbage within the sward and its physical composition. Very little work apart from that of Theron and Boysen (1966) has examined the physical attributes of herbage relative to a preference ranking, though Evans (1964) quotes Beaumont, Stitt and Snell (1933) as having found inter-specific leaf strength differences associated with palatability. Hendricksen and Minson (1980) suggested that low intakes by cattle grazing a sub-tropical legume were possibly associated with the high shear loads needed to harvest the stems after the leaves had been preferentially removed.

The position of herbage components within the sward may determine how readily they are grazed, depending on the species of grazing animal involved. Grazing ruminants have broadly similar mouthparts in which the upper incisors are missing but are replaced instead by a firm dental pad against which the teeth grip the herbage during grazing. Descriptions of the mouthparts are to be found in Sissons and Grossman (1975). There are, however, differences between animal species which have important repercussions on manipulative ability. Bovine species have thick,wide lips which are comparatively immobile, whilst sheep have thin, mobile lips, the upper of which is marked by a distinct philtrum. In contrast to the sheep the tongue of the cattle is protractile and is used in the prehension of herbage. Chambers, Hodgson and Milne (1981) found that the ratio of jaw movements to biteswas greater in grazing sheep than in grazing cattle suggesting that the sheep manipulated the herbage with their lips and jaws before biting to a greater extent than cattle.

Bell (1969) found that there were marked differences between grazing and browsing species in the shape of the anterior end of the mandibles and the angle of insertion of the incisors. In the browsers the incisors meet the palate nearly at right angles enclosing a deep cavity. In the grazers the incisors are inserted into the mandibles at such an angle that when the mouth closes the teeth lie almost flat against the palate. Bell (1969) suggested that browsers pull the stems of the dicotyledenous plants on which they feed through their mouths, scraping the leaves off into the cavity behind the incisors. The dentition of the sheep follows that outlined above for browsing animals in that the incisors form a narrow, strongly curved arch. The feeding behaviour described for browsers has also been observed in sheep grazing lucerne (Arnold, 1966). Cattle, whose incisors are set in a fan, use their tongue to sweep herbage into their mouths (Johnstone-Wallace and Kennedy, 1944; Hafez, 1969; Gordon, 1970) and then clamp the herbage between the dental pad and incisors before tearing it off. It has been suggested that the tongue may also be used to grip the herbage against the incisors rather than the dental pad. (Chambers, Hodgson and Milne, 1981). Sheep do not use their tongues to prehend herbage but clamp the material between incisors and dental pad and then sever it with a quick upward jerk of the head. Leigh (1974) suggested that cattle cannot graze closer to the ground than 12 mm due to the structure of the lower jaw, whilst other workers have suggested that sheep can graze closer to the soil surface than cattle (Dudzinski and Arnold, 1973). Ellis and Travis (1975) suggested that pronghorn antelope were more selective than cattle on the basis that the muzzle of the antelope is long and narrow, with a cleft upper lip similar to sheep, in contrast to the broad mouth of the cattle. Jamieson and Hodgson (1979b) could find no evidence that lambs were better adapted than calves to deal with short swards. Allden and Whittaker (1970) however suggested that, where swards were short, small-mouthed lambs might have a competitive advantage over bigger mouthed adults.

The evidence suggests that animals with narrow muzzles and mobile lips are more selective than broad-muzzled species which use their tongues to gather herbage. The differences in the diets are likely to be greatest where the sward structure is such that narrow-muzzled species have a greater opportunity to select components out of the sward than broad-muzzled species. Apart from the work of Gwynne and Bell (1968), Bell (1969) and Ellis and Schwartz (1981) there have been few studies that have attempted to explain the ecological separation of grazing animals in terms of opportunity for selection.

Conclusions

In section I it was shown that the intake per bite and the rate of biting of grazing animals was influenced by the sward structure. Ultimately it is the degree of selection carried out by the animal that influences intake per bite and rate of biting. There appear to be no published studies on cattle and sheep grazing together that relate the ingestive behaviour variates of intake per bite, rate of biting and grazing time to measurements of sward structure under conditions where the opportunity for selection is likely to reveal large differences between the tactics of cattle and sheep.

EXPERIMENT 1

Comparative studies on the influence of sward conditions on the ingestive behaviour of sheep and cows

Introduction

The influence of sward structure on various aspects of ingestive behaviour, particularly rate of biting, grazing time and weight per bite has only recently been examined (Stobbs, 1973 a & b; Jamieson, 1975; Chacon and Stobbs, 1976; Jamieson and Hodgson, 1979 a & b; Hodgson, 1981; Wade and Le Du, 1981). Only Jamieson (1975) and Jamieson and Hodgson (1979b) have compared differences in ingestive behaviour between sheep and cattle. These and other studies (Arnold, 1964 ; Hodgson, 1968; Allden and Whittaker, 1970) have shown that the herbage intake of grazing animals may be strongly influenced by variations in the structure of the sward.

This experiment was designed to compare and contrast the ingestive behaviour responses of cattle and sheep to variations in sward structure under controlled conditions prior to the main study. The swards used in this experiment were relatively simple in structure and botanical composition, in contrast to the complex, indigenous swards of Experiment 3.

Table E1.1

The design of Experiment 1

Treatments	Levels
Animal species	Cattle ; Sheep
Sward structure	Dense ; Open
Periods	Week 1 ; Week 2
Sub-periods	Sub-period 1 ; Sub-period 2
Groups within animal species	Fistulated ; non-fistulated

Fistulated animals were transferred between swards between sub-periods within weeks, but were not transferred between swards between weeks.

Non-fistulated animals were not transferred between swards within weeks, but were transferred between swards between weeks.

Materials and Methods

Location

The experiment was carried out at the Hill Farming Research Organisation's Glensaugh research station (latitude 56°54'N, longitude 2°32'W) over the weeks 24-28th July and 31st July - 4th August 1978. The swards lay on a south facing slope at an altitude of 150 m. The soil type is a brown forest soil of the Strichen Association. The average annual rainfall (at 195 m) is 1041.4 mm.

Experimental design

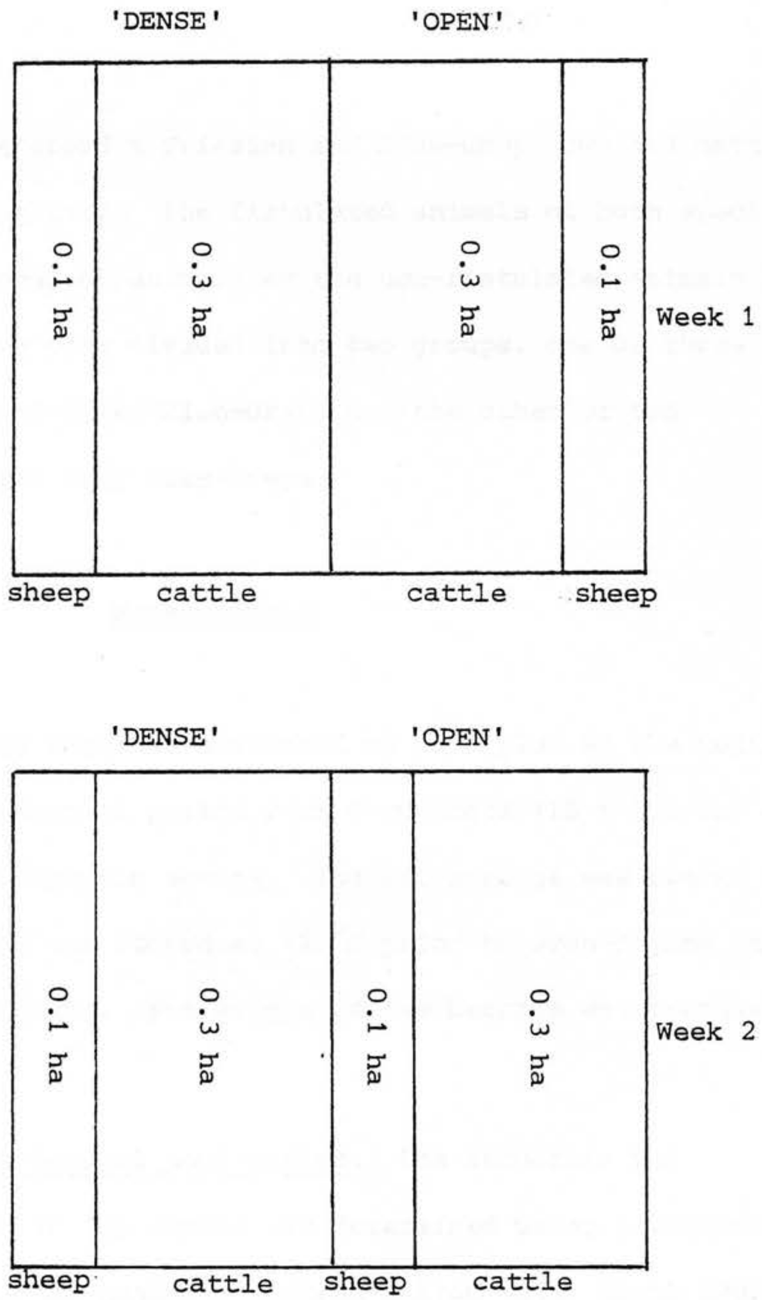
The design of the experiment is shown in Table E1.1. Two swards contrasting in structure were grazed separately by cows and sheep over two successive five-day periods, the second period acting as a replicate. Each sward was subdivided into two plots, in the ratio of 3:1 as in Figure E1.1, giving in total 8 sub-plots, the larger sub-plots (0.3 ha) being grazed by the cows and the smaller (0.1 ha) by the sheep. Four grazer cows and two oesophageal fistulate cows grazed on each cow plot. Four grazer wethers and four oesophageal fistulate wethers grazed each sheep plot, and between two and four extra wethers were used to balance the grazing pressure between cow and sheep plots. The fistulated animals were transferred between pairs of swards on the third day in each week. Non-fistulated animals were re-allocated to swards between weeks but fistulated animals remained on the same swards until re-allocation on the third day. Animals were not re-randomised between groups between weeks. For two weeks prior to the experiment the animals grazed perennial ryegrass swards of broadly similar composition.

Swards

The swards were of perennial ryegrass, with little clover, (less than 1%). The contrasting 'open' and 'dense' sward structures were

Figure E1.1

The layout of plots in Experiment 1



obtained by mob-stocking with sheep for two or three days at weekly intervals in the case of the 'dense' sward and at monthly intervals in the case of the 'open' sward, in 1977 and again in early 1978.

Three weeks prior to the experiment 60 kg N/ha was applied to both swards as 20:10:10 compound and they were trimmed with a forage harvester, the trimmings being collected and removed.

Animals

Mature barren Hereford x Friesian and Blue-Grey cows and mature Blackface wethers were used. The fistulated animals of both species came from the same group of animals as the non-fistulated animals. The two breeds of cows were divided into two groups, one of three Hereford x Friesian and three Blue-Greys and the other of two Hereford x Friesian and four Blue-Greys.

Measurements

Sward measurements

Herbage mass: Herbage mass was estimated on each plot at the beginning and end of each experimental period from 6 quadrats (15 x 122 cm) cut to ground level with electric shears. The cut herbage was placed in self-seal plastic bags and stored at $-20^{\circ}C$ prior to oven-drying at $80^{\circ}C$ for 36h, and weighing. The weight of the herbage was expressed as kg DM/ha.

Sward structure and botanical composition: The structure and botanical composition of the swards was determined using a combination of inclined (32.5°) point quadrats (Warren-Wilson 1963, Grant 1981) and horizon sampling techniques (Rhodes, 1981). With the point quadrat all contacts were recorded as the needle passed through the sward and each contact was identified in terms of species, morphological unit and whether live or dead . The data obtained can be set

Figure E1.2

Horizon sampling equipment

A= Cutting head and vacuum cleaner attachment

B= Movable rest for cutting head

C= Adjustable frame

out graphically to illustrate the height/density relationships of the swards (Spedding and Large, 1957). Horizon sampling was carried out using the equipment illustrated in Figure E1.2, which consisted of an adjustable frame on which rested electric shears which could be moved forward and backwards so as to cut a defined area at any specified height. The cut herbage was collected by a modified vacuum cleaner, attached to the cutting head. Four quadrats were cut per plot, the horizons being cut at 3 cm intervals. The material cut from each horizon was stored at -20°C prior to separation into the following herbage components; green grass leaf, green grass vegetative stem, green grass flower stem and flower, clover, other dicots and total dead. After separation each fraction was dried at 80°C for 36h. Each fraction was then converted to kg DM/ha/horizon.

Sward height: Sward height was estimated from both surface and extended height measurements. Surface height was measured by recording the height of the tallest leaf, stem or flower to touch a ruler or graduated pin inserted, with minimum disturbance, into the sward. Extended height was measured by extending to full length the same component used to determine surface height as described by Hodgson *et al* (1971). Thirty measurements were made per plot.

Pattern of defoliation: The pattern of defoliation was estimated after grazing from sward surface height measurements made at 5 cm intervals along transects laid diagonally from corner to corner across the long axis of each plot.

Animal measurements

Live weight: The animals were routinely weighed before and after each experiment.

Diet digestibility: The digestibility of the diet selected was estimated from samples of extrusa collected by oesophageal-fistulated animals. Fistulae were established, and the animals subsequently maintained, largely as described by Rodriguez (1973). The fistulated animals belonged to the same group of animals as the non-fistulated animals used in the experiment. All the fistulae were well established (at least 2 years) and all fistulated animals had been used in previous experiments. Samples of extrusa were collected on the first two and last two days of each week in the following manner. The animals were brought into a handling pen at 09.00h and the split-plugs removed. The fistulae were thoroughly washed and a foam-rubber plug on a cord was inserted into the oesophagus just below the fistula to ensure 100% recovery (Stobbs, 1973a). The cord was then tied around the animal's neck to prevent the plug being swallowed. A suitably sized polythene bag with the sides split to within a few centimetres of the bottom was then positioned over the fistula and fastened around the animal's neck. The bags were prevented from slipping forward during grazing by attaching the bag by clips and cord to a girth-strap on the animal. The animals were turned out to graze in pairs, thus allowing the preparation of the second pair of animals whilst the first pair were collecting samples. Once a sufficient sample had been gathered (between 500 and 1000g wet weight for the cattle and 100 to 500g wet weight for the sheep) the animals were returned to the handling pen. The time taken to collect a sufficient sample was seldom longer than 10 minutes, and generally if no sample had been collected in 15 minutes the animal or animals concerned were returned to the handling pen. In the handling pen the bags were removed along with the throat-plugs and any extrusa still in the oesophagus was collected. The split-plugs were replaced in the fistula and animals which had provided samples were returned to their plots. Animals which did not provide samples had their split-plugs replaced but were not returned to their plots but were sampled again within two or three hours. The extrusa samples were placed into self-seal polythene bags and frozen immediately with solid carbon dioxide. They were then stored at $-20^{o}C$ until they could be processed. Any samples which appeared to be contaminated with rumen contents were discarded. The frozen extrusa samples were broken up and divided into two portions, one of which was freeze-dried and then ground through a 0.4 mm sieve. This portion was then analysed for organic matter digestibility (OMD) (Alexander and McGowan, 1965) and ash. The second portion was retained for the determination of botanical composition.

Since oesophageal-fistulated animals are used to determine diet OMD, which is used subsequently in the estimation of the herbage intake of non-fistulated animals it is important to ascertain whether or not there are differences in the diets selected by fistulated and non-fistulated animals which might influence the diet OMD, and hence the intake estimates. Appendix 5 describes the results of a trial carried out during Experiment 3 which examined the differences between the diets of the fistulated and non-fistulated animals by means of faecal cuticle analysis.

Weight per bite: The weight of herbage taken in individual bites was determined using the oesophageal fistulated animals while collecting extrusa samples for the determination of OMD and botanical composition. The procedure involved counting the number of bites taken during the collection of the samples. Since the animals were run in pairs two people were required, but preliminary tests had shown good agreement between the individuals involved in counting bites. It was assumed that the use of throat-plugs used as described above resulted in complete recoveries of extrusa. The weights per bite were calculated by dividing the weight of the sample by the number of bites taken. To aid comparison between the cattle and sheep the weights per bite were expressed as mg OM/bite/kg LW.

Rate of biting: Rates of biting were obtained for all animals using the 20 bite method of Jamieson (1975). Biting is characterized by the sound of the herbage being severed and the distinctive upward jerk of the head. Measurement of rate of biting consisted of recording, by stop-watch, the time taken to complete 20 bites. Measurements were discarded if animals lifted their heads to walk any distance or to scratch, look around about, defecate or urinate. Recording continued if the animal walked a few paces with its head down whilst obviously selecting herbage, and also continued if the head was lifted while chewing herbage in between bouts of biting. Paired measurements were made on each animal during the major grazing periods of each day, which were roughly dawn, mid-morning, early afternoon, late afternoon and dusk. Prior to analysis the mean daily rate of biting was calculated after conversion of the time per 20 bites to bites per minute. The above method is a slight adaptation of Jamieson's (1975) and probably more closely approximates the mean daily rate of biting than Jamieson's which provides an indication of the probable maximum rate of biting.

Grazing time: Grazing time was measured using Kienzle vibracorders (allden, 1962; Stobbs,1970) attached to the heads of the cattle and the shoulders of the sheep, and bite-meters (Chambers, Hodgson and Milne, 1981). Two animals of each species wore vibracorders and two wore bite-meters, the instruments being exchanged between pairs of animals between weeks. Vibracorder charts were replaced at 08.30h on each morning, and bite-meters were read and reset at the same time. The vibracorders were waterproofed by slipping broad rings cut from small motor-car inner tubes over the join between the two halves of the instruments.

Diet composition: The botanical composition of the diets selected by the fistulated animals was analysed by separation of the second portion of the extrusa samples. The samples were separated into the following categories of live and dead material: grass leaf, grass vegetative stem, grass flower stem and flower, clover, other dicots and debris. The separated fractions were dried for 36h at 80°C and weighed and the respective weights and proportions of the components in the whole sample were calculated.

Statistical analyses

The measurements of herbage mass, sward height, diet digestibility, weight per bite, rate of biting, grazing time, and diet composition were analysed by analysis of variance (ANOVA) using the EDEX programme developed by Hunter, Patterson and Talbot (1973). Split-plot and split-split-plot designs were used. Missing values were not calculated due to the sometimes large proportions of missing values and the consequent inaccuracy of the calculated values. The lack of calculated values to replace missing values resulted in unequal frequencies of values in many of the tables of means. Consequently the presentation of tables of means differs somewhat from the conventional presentation. Where necessary the numbers (n) of values in each mean are given along with standard errors of difference (SED). Two-way tables are given irrespective of their significance in the ANOVA table. Normally SED values are given as non-significant (NS) where the F-test for that table indicates NS.

The pattern of defoliation results were analysed using a generalized linear modelling programme, GLIM. (Nelder, 1974) in which the variances of the mean sward heights (taken from the height measurements along the transects) on each of the plots were used as the data base. The results are presented as a table giving the terms fitted in the

Table E1.2

The mean herbage mass (kg DM/ha) of the plots grazed by the cattle and sheep on the 'dense' and 'open' swards before and after grazing in weeks 1 and 2 †

Week 1

Swards		Pregrazing	Postgrazing
'Dense'	Cattle	3910	3120
	Sheep	3847	3309
'Open'	Cattle	4196	3254
	Sheep	3201	3165

Week 2

Swards		Pregrazing	Postgrazing
'Dense'	Cattle	4277	4080
	Sheep	4053	3371
'Open'	Cattle	4071	3031
	Sheep	4654	3013

SED where equal replicates = 509.5 NS

SED where unequal replicates = 624.0 NS

† values are means of 6 quadrats except for cattle pregrazing the 'open' sward in week 1 where only 3 quadrats were cut

model, the degrees of freedom and the deviances. The deviance is the log-likelihood ratio of the current model, the distribution of which for data with a Gamma distribution (as is the case here) is approximately proportional to χ^2.

Results

The results presented here follow the sequence of sward and animal measurements described in the materials and methods section. No results are presented for data collected by the bite-meters since few acceptable records were collected with this equipment.

Sward measurements

Herbage mass: Table E1.2 gives the herbage mass (kg DM/ha) in the cattle and sheep plots on the different swards in weeks 1 and 2 of the experiment both before and after grazing. Overall there was less herbage on the swards grazed in week 1 than in week 2 (3454 vs 3819; $P < 0.05$), and a reduction in herbage mass as a result of grazing (4015 vs 3293; $P < 0.001$). The full results of the ANOVA are given in Appendix Table E1.1.

Sward structure and botanical composition: Due to the large number of individual horizon samples which had to be separated, quadrats were bulked within plots to give one sample per plot consisting of between 4 and 9 horizons prior to separation of the individual horizons. Analysis of variance was carried out for each of the herbage components in each horizon, with the exception of the clover, other dicots, and debris components which were negligible. Weeks were used as replicates in the analysis. The total weights of the herbage components in the cattle and sheep plots on each sward are given in Table E1.3 The analysis of variance on the total weights of the herbage components in the swards (Appendix Table E1.2.1 to E1.2.4) shows that the effect

Table E1.3

The total weights (kg/ha) of green leaf, green vegetative stem, green flower stem and flower and total dead in the swards †

Green leaf

	Pregrazing		Postgrazing	
Swards	Cattle	Sheep	Cattle	Sheep
'Dense'	2019	1644	908	895
'Open'	2088	1749	1070	920

SE ± 228.7 NS

Green vegetative stem

	Pregrazing		Postgrazing	
Swards	Cattle	Sheep	Cattle	Sheep
'Dense'	784	803	1139	599
'Open'	560	663	1081	672

SE ± 89.6 NS

Green flower stem and flower

	Pregrazing		Postgrazing	
Swards	Cattle	Sheep	Cattle	Sheep
'Dense'	297	435	204	299
'Open'	539	206	167	146

SE ± 55.0 NS

Total dead

	Pregrazing		Postgrazing	
Swards	Cattle	Sheep	Cattle	Sheep
'Dense'	780	899	1252	1005
'Open'	1104	676	1227	503

SE ± 197.0 NS

† Since each value is the mean of 2 measurements the SE and not the SED is given in this table

Table E1.4

The mean height of the herbage in the cattle and sheep plots on the 'dense' and 'open' swards

		Plots	
Swards	Cattle	Sheep	SE
Dense	18.7^{a}	15.1^{ac}	
			± 0.72
Open	17.9^{b}	20.5^{bc}	
SE	± 0.62		

Mean of two weeks †

\+ Since the numbers of values contributing to each mean are equal (n = 60) the SE and not the SED is given in this table. Values with the same superscript are significantly different ($a = P < 0.001$, $b = P < 0.05$, $c = P < 0.001$).
Diagonal comparisons are not relevant.

of grazing was only significant for green leaf (1875 vs 949 ± 114.4; $P < 0.01$) and that there was a significant interaction between grazing and plots for green vegetative stem. The weights of each component in each horizon are given in Appendix tables E1.3.1 to E1.3.4.

The vertical distributions of the sward components before and after grazing are given graphically in Figures E1.3.1 to E1.3.8 by plotting in each 5 cm horizon for each component the contacts per 100 points, following the method of Spedding and Large (1957).

Sward height: The mean height of the swards in the cattle and sheep plots prior to grazing is given in Table E1.4. The interactions of swards x plots and weeks x plots were significant ($P < 0.001$ and $P < 0.01$ respectively). The main sward effect was also significant with the 'dense' sward being significantly shorter than the 'open' sward (16.9 vs 19.2; $P < 0.001$). The results of the ANOVA are given in Appendix Table E1.4.

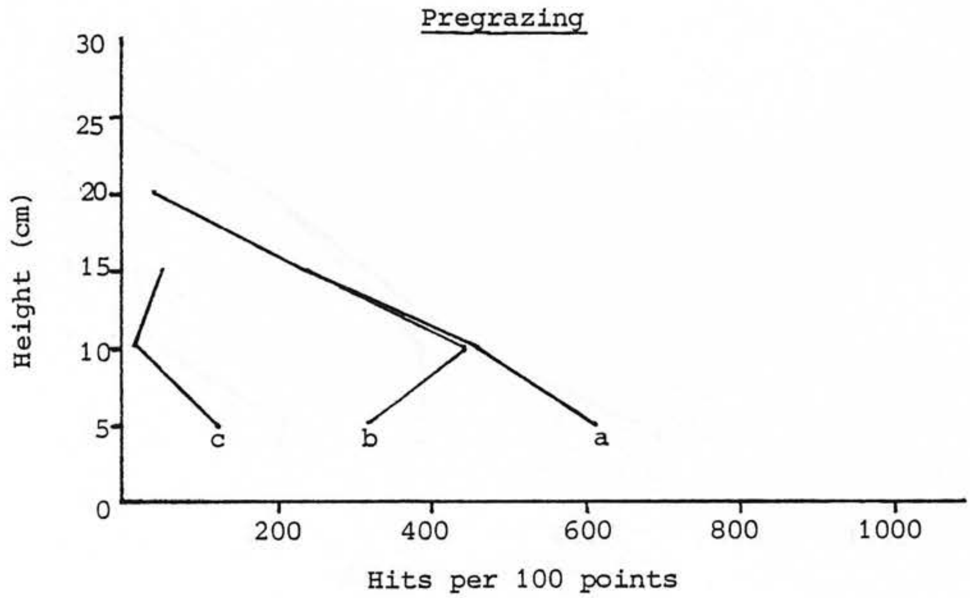
Pattern of defoliation: The results of the analysis of the variances of the mean sward heights after grazing are given in Appendix Table E1.5 along with the mean heights of the swards. Appendix Figure E1.1 illustrates the different patterns of defoliation on the sheep and cattle grazed swards.

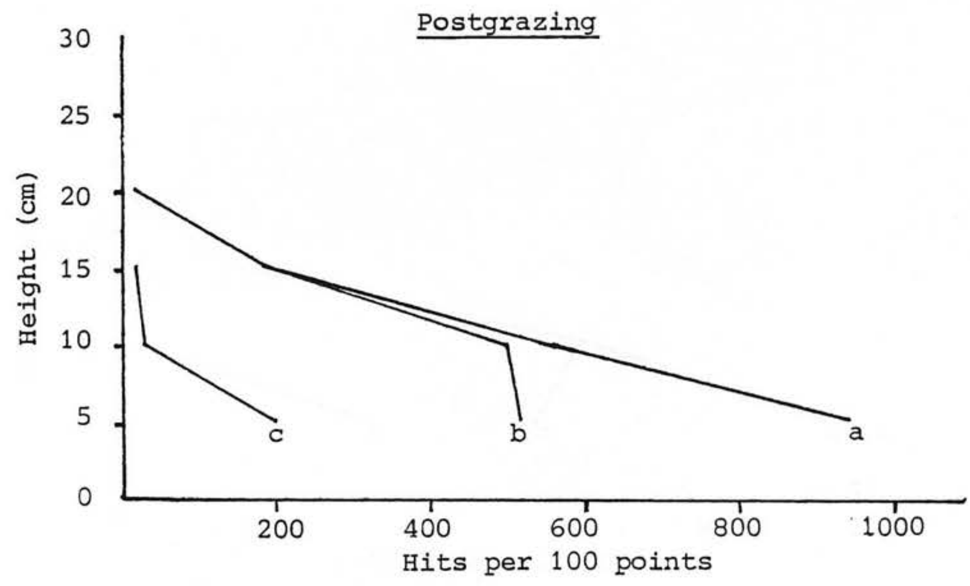
Animal measurements

Diet digestibility: The mean OMD of the diets selected by the oesophageal fistulated cattle and sheep on the different swards, meaned over weeks, periods within weeks and days within periods are presented in Table E1.5. The ANOVA result is given in Appendix Table E1.6. The interaction of animal species x periods within weeks x days within periods was significant ($P < 0.05$). Diet digestibility was lower in Week 2 than in Week 1 (0.79 vs 0.78; $P < 0.05$), and sheep selected a more digestible diet than cattle (0.79 vs 0.77; $P < 0.001$).

Figure E1.3.1

The vertical distribution of herbage components in the 'Dense' sward before and after grazing by the sheep in the first week





a = total green and dead hits

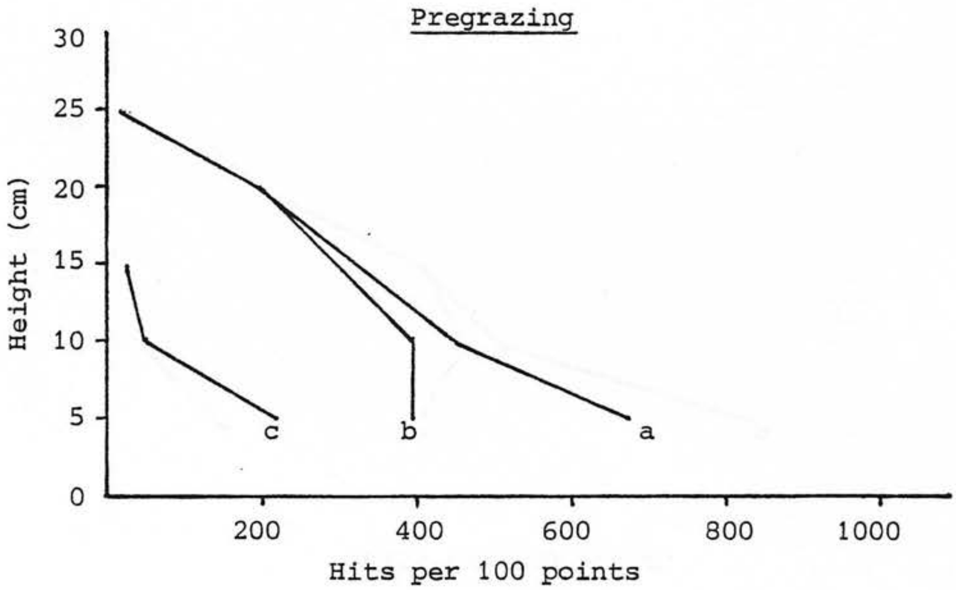
b = total green hits

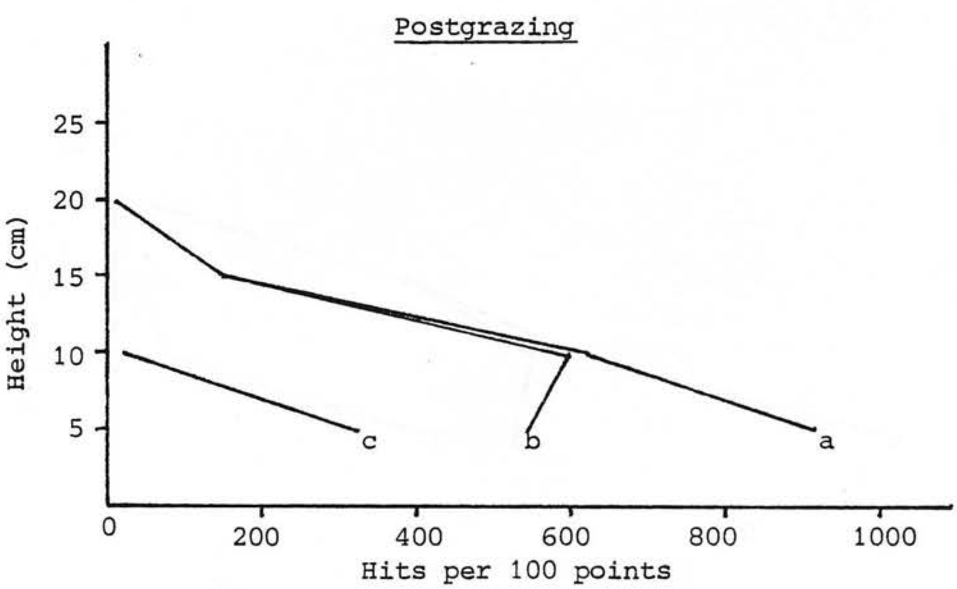
c = green stem + flower hits

b-c = green leaf

Figure E1.3.2

The vertical distribution of herbage components in the 'Dense' sward before and after grazing by the cattle in the first week.





a = total green and dead hits

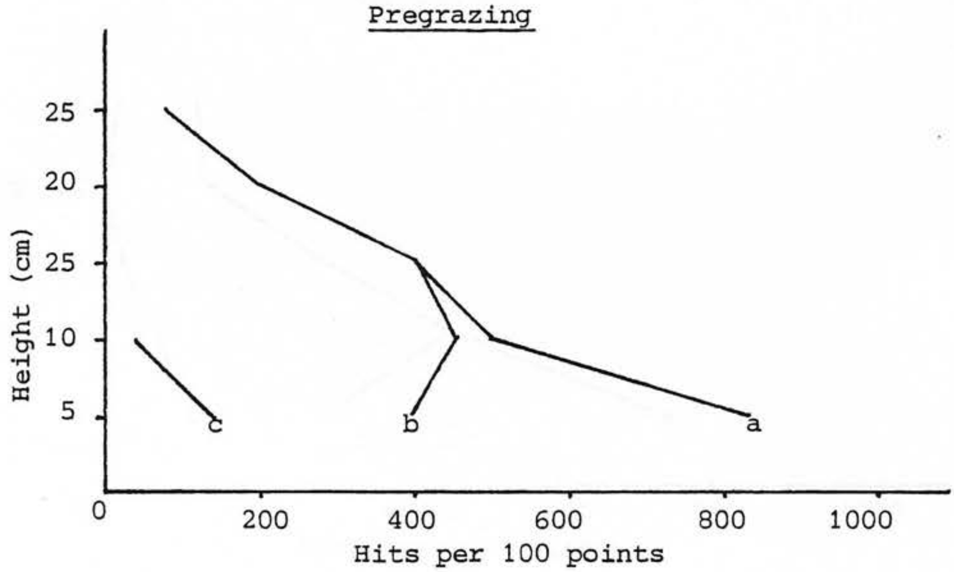
b = total green hits

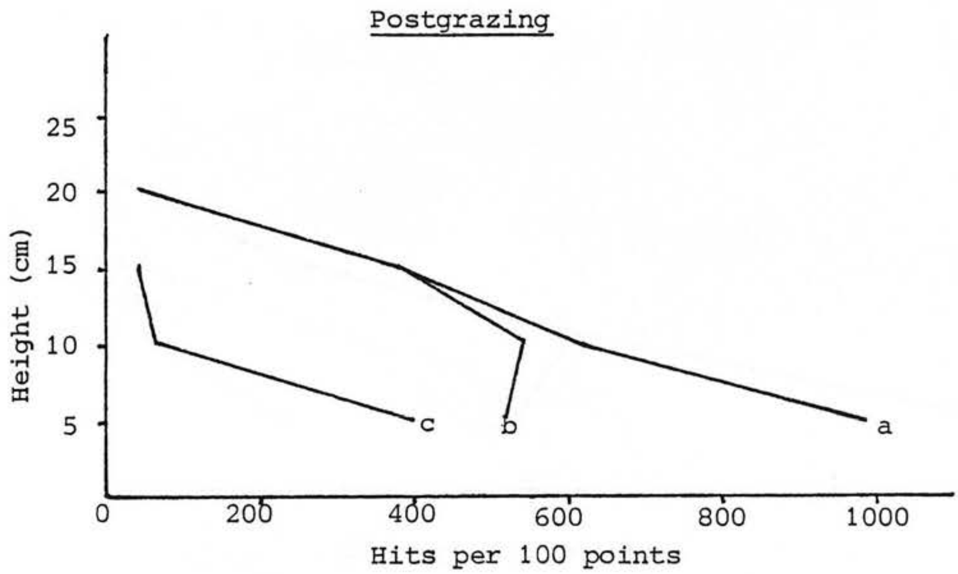
c = green stem and flower hits

b - c = green leaf

Figure E1.3.3

The vertical distribution of herbage components in the 'Open' sward before and after grazing by the sheep in the first week.





a = total green and dead hits

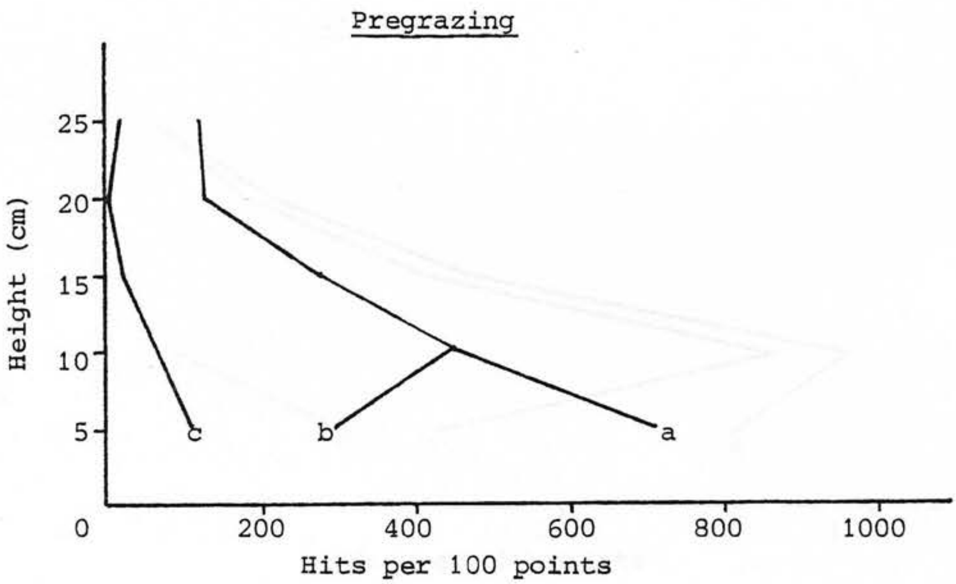
b = total green hits

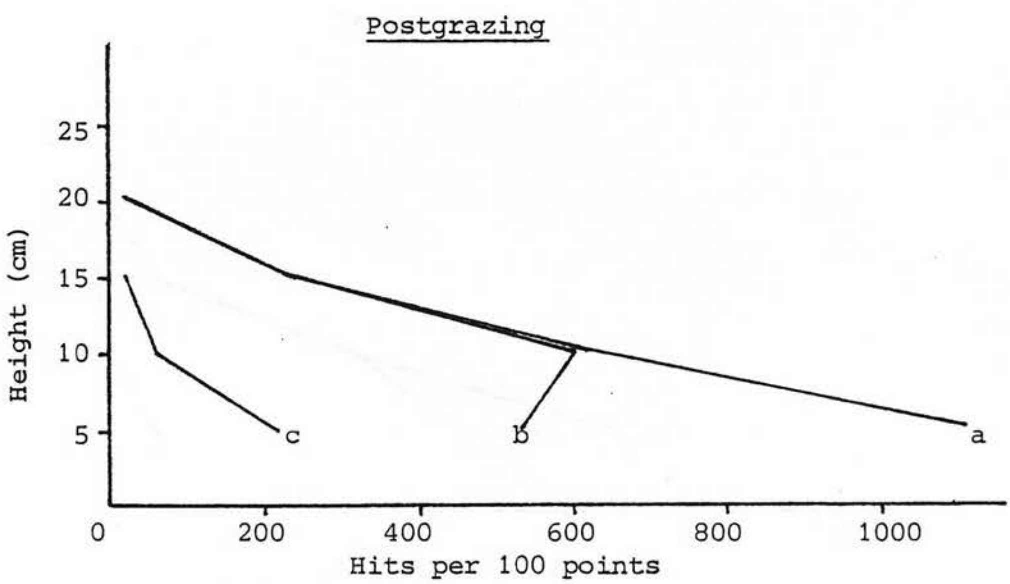
c = green stem and flower hits

b - c = green leaf

Figure E1.3.4

The vertical distribution of herbage components in the 'Open' sward before and after grazing by the cattle in the first week.



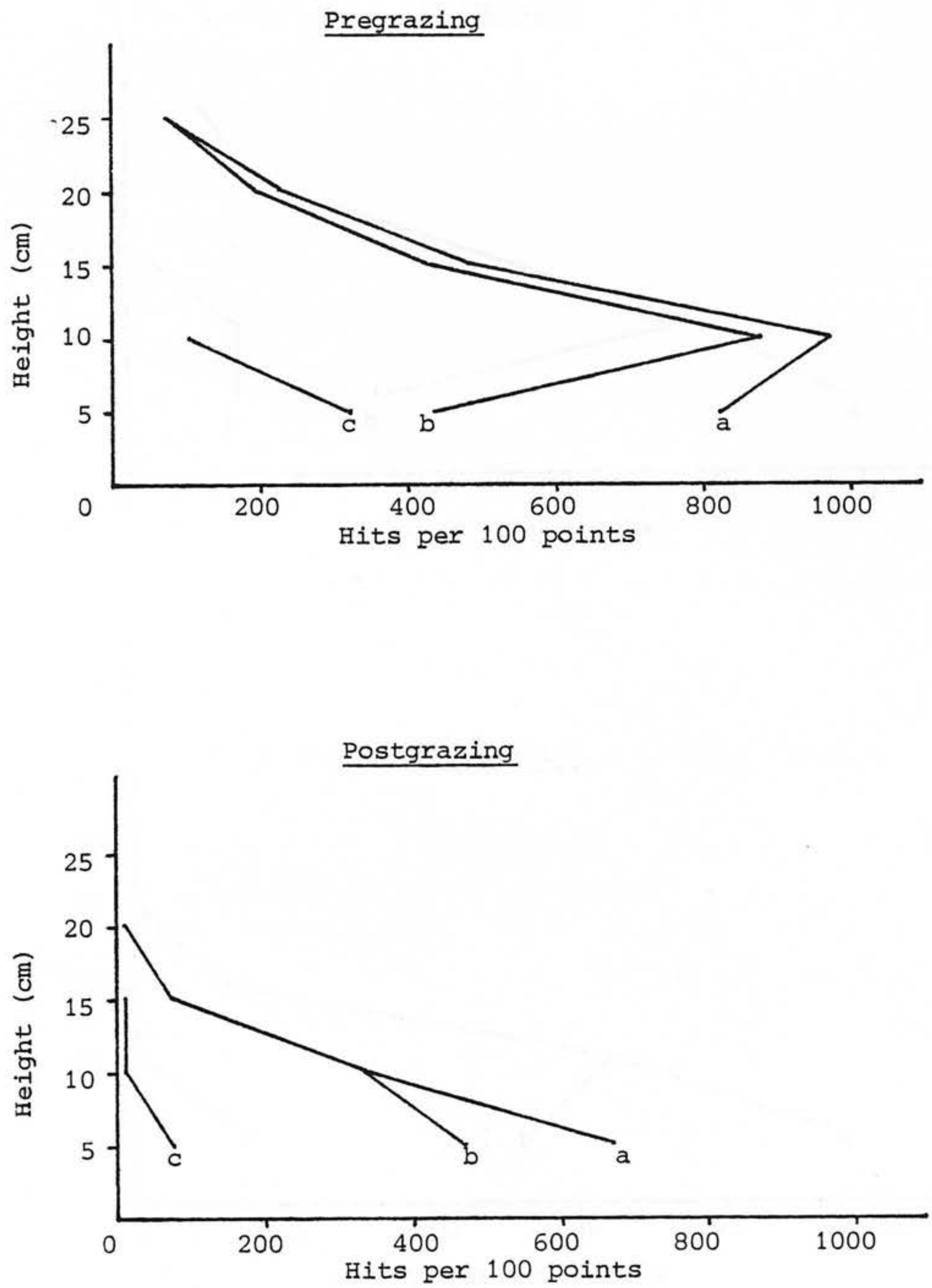


a = total green and dead hits
b = total green hits
c = green stem and flower hits

b - c = green leaf

Figure E1.3.5

The vertical distribution of herbage components in the 'Dense' sward before and after grazing by the sheep in the second week.



a = total green and dead hits

b = total green hits

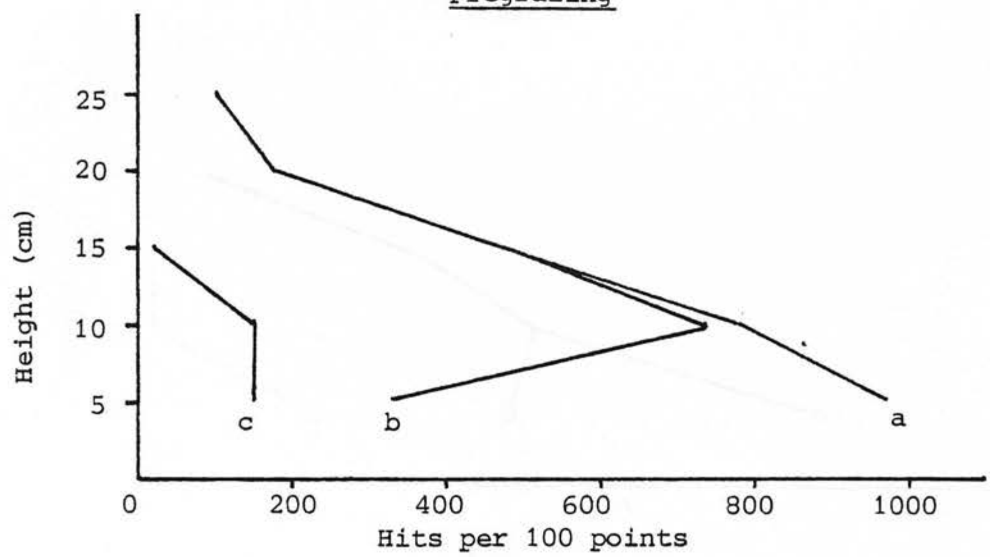
c = green stem and flower hits

b - c = green leaf

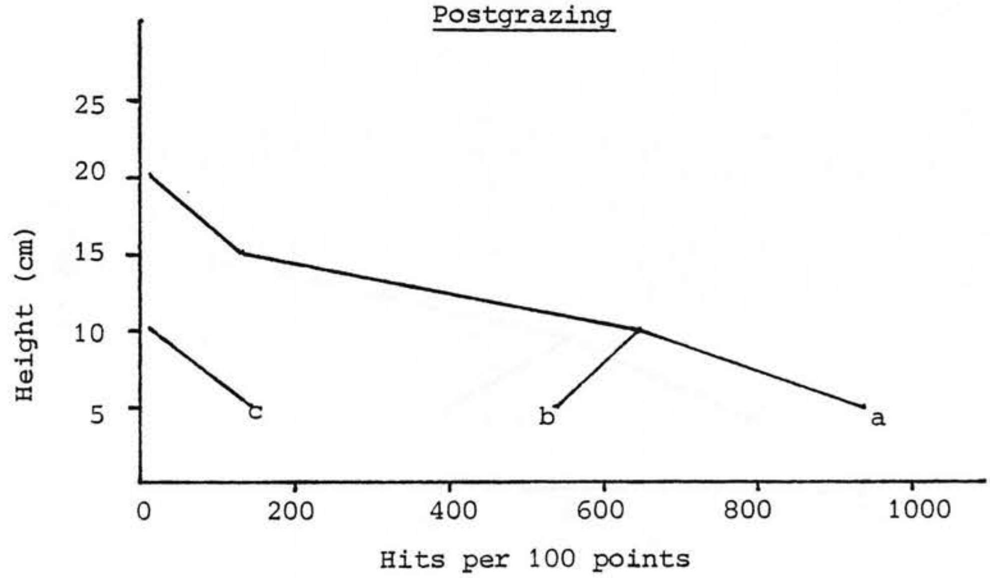
Figure E1.3.6

The vertical distribution of herbage components in the 'Dense' sward before and after grazing by the cattle in the second week

Pregrazing



Postgrazing

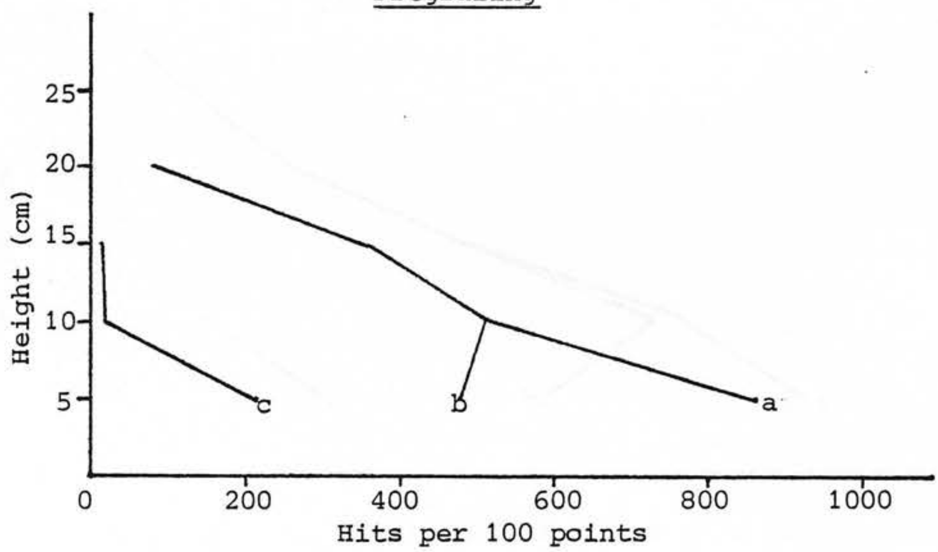


a = total green and dead hits
b = total green hits
c = green stem and flower hits
b - c = green leaf

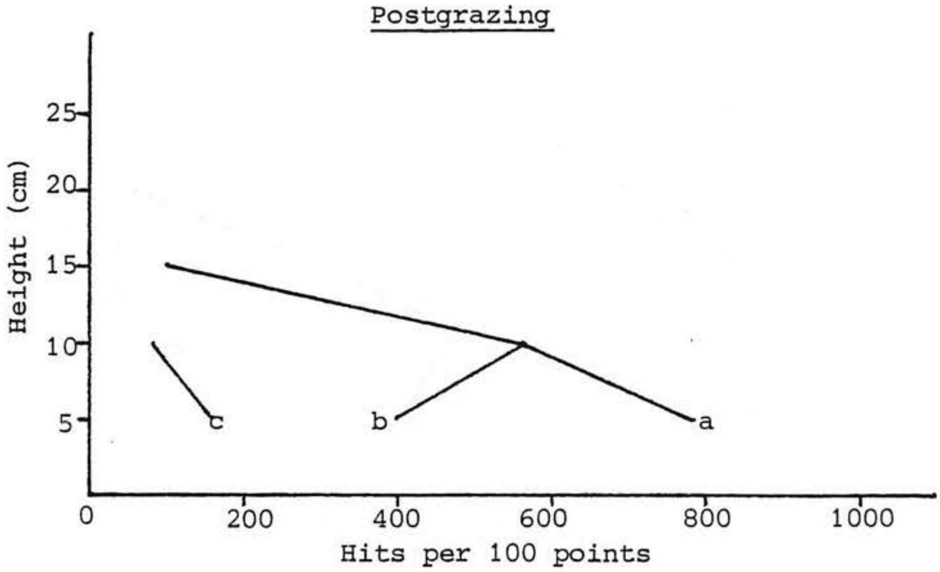
Figure E1.3.7

The vertical distribution of herbage components in the 'Open' sward before and after grazing by the sheep in the second week

Pregrazing



Postgrazing

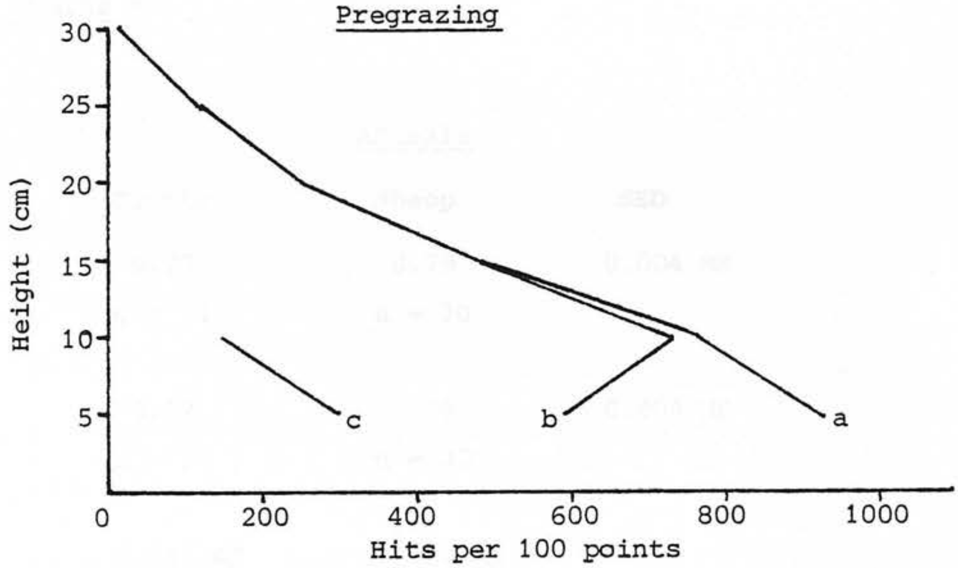


a = total green and dead hits
b = total green hits
c = green stem and flower hits
b - c = green leaf

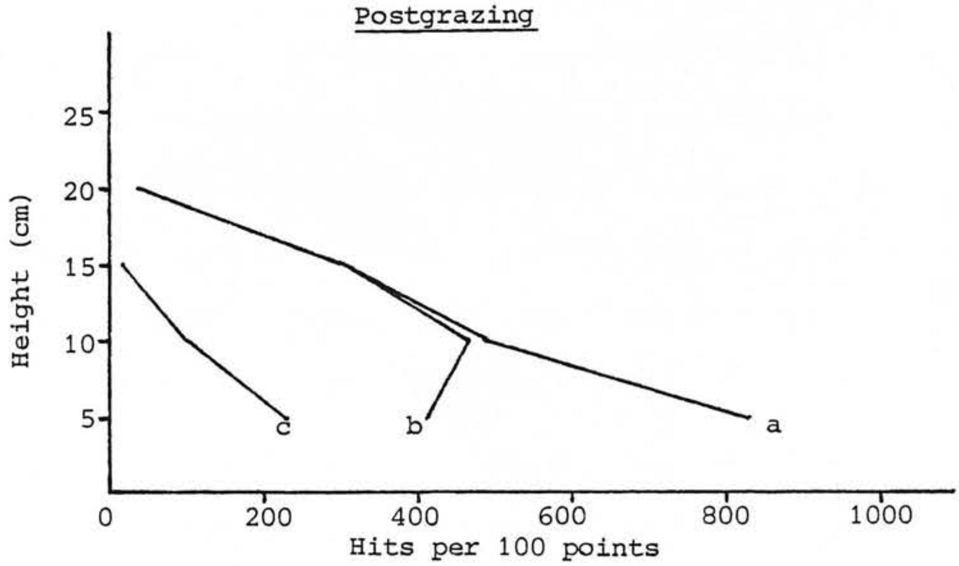
Figure E1.3.8

The vertical distribution of herbage components in the 'Open' sward before and after grazing by cattle in the second week

Pregrazing



Postgrazing



a = total green and dead hits

b = total green hits

c = green stem and flower hits

b - c = green leaf

Table E1.5

The organic matter digestibility (OMD) of the diets obtained by the cattle and sheep grazing the 'dense' and 'open' swards *

Swards	Animals		
	Cattle	Sheep	SED
'Dense'	0.77 n = 15	0.79 n = 30	0.004 NS
'Open'	0.77 n = 16	0.79 n = 30	0.004 NS
SED	0.005 NS	0.004 NS	

* Means of days, periods and weeks

Figure E1.4 illustrates the mean change in the OMD of the cattle and sheep extrusa on the two swards over successive days.

Weight per bite: The mean weight of herbage taken per bite (mg OM/bite/kg LW) by the cattle and sheep in the two sub-periods on the two swards meaned over the two weeks is given in Table E1.6. The ANOVA result is given in Appendix Table E1.7. Only the effect of periods within weeks was significant ($P < 0.05$). Figure E1.5 illustrates the decline in weight per bite by the animals as grazing continued.

Rate of biting: The rates of biting by the cattle and sheep are summarised in Table E1.7. The ANOVA result is given in Appendix Table E1.8. The interactions of animal species x swards, animal species x days and animal species x swards x days were significant ($P < 0.05$, $P < 0.001$ and $P < 0.05$ respectively). Cattle grazed significantly faster than sheep overall (61 vs 50; $P < 0.001$) and there were significant differences between days ($P < 0.05$). Mean rates of biting by individual animals within species were not significantly different. Figure E1.6 shows the changes in rates of biting by the cattle and sheep on successive days meaned over the two weeks. For the cattle on the 'dense' sward no between-day differences were significant, whilst on the 'open' sward only differences between day 5 and days 1 and 4 were significant ($P < 0.05$). For the sheep on the 'dense' sward day 4 was significantly ($P < 0.05$) different from days 2 and 3, with no other differences being significant. On the 'open' sward days 3, 4 and 5 were significantly ($P < 0.05$) different from day 1 alone.

Grazing time: Table E1.8 presents the mean grazing times of the cattle and sheep on the different swards. Differences between individuals within species were not significant. The animal species x sward interaction was significant ($P < 0.05$) but the other main effects apart from that of the swards ($P < 0.05$) were not significant. Mean grazing time

Figure E1.4

Organic matter digestibility of the cattle and sheep diets on successive days while grazing the 'Dense' and 'Open' swards. (No measurements made on day 3. Values are means of 4 animals x 2 weeks).

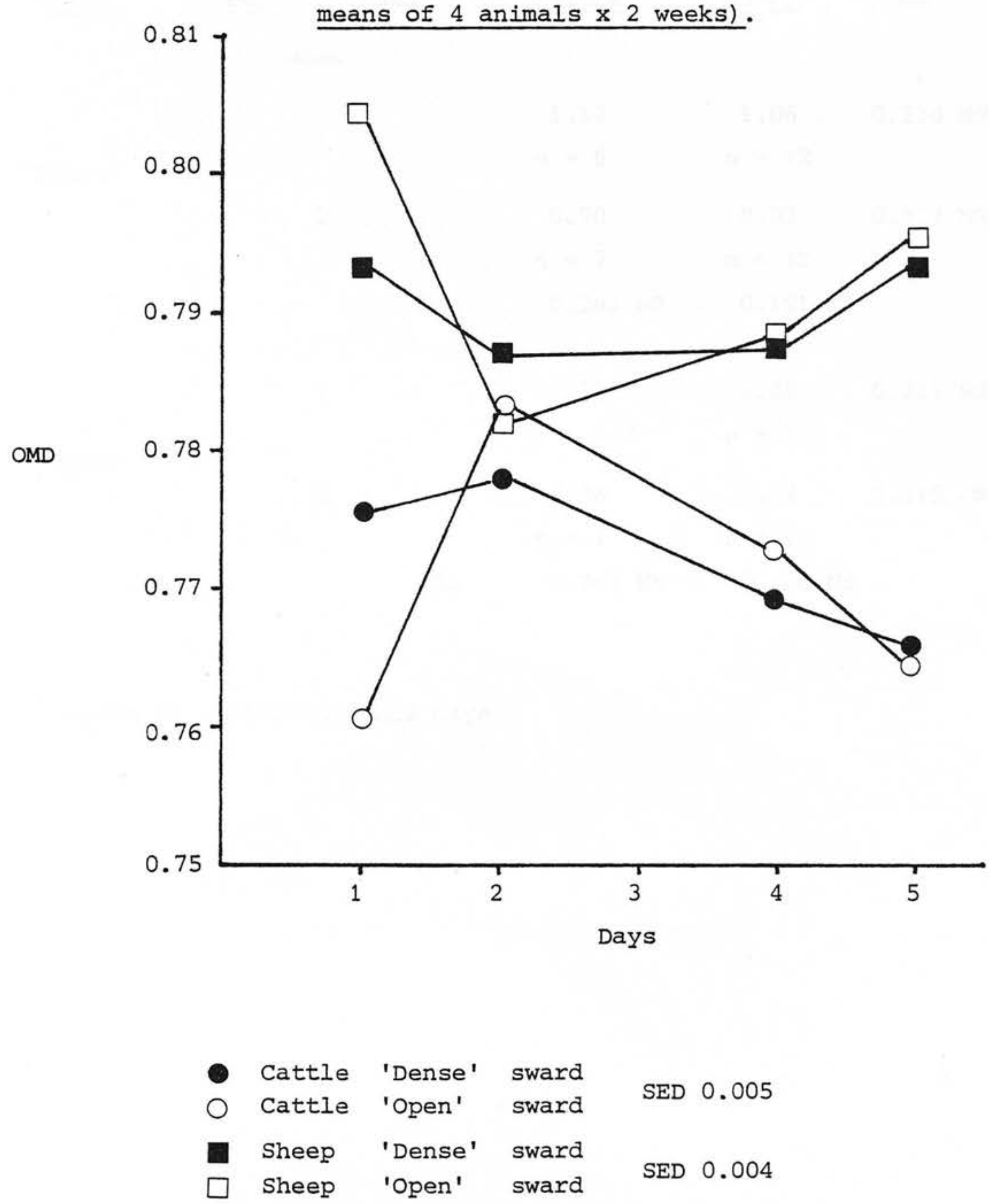


Table E1.6

Mean weights per bite (mg OM/bite/kg LW) of the cattle and sheep on the 'dense' and 'open' swards in the two within week periods

Sward	Period within week		Cattle	Sheep	SED
'Dense'	1		1.12	1.06	0.234 NS
			n = 6	n = 12	
	2		0.70	0.93	0.223 NS
			n = 7	n = 12	
		SED	0.261 NS	0.191 NS	
'Open'	1		1.38	1.32	0.231 NS
			n = 6	n = 13	
	2		0.96	1.02	0.215 NS
			n = 7	n = 15	
		SED	0.261 NS	0.178 NS	

† Means of individuals and days

Figure E1.5

Weights per bite of the cattle and sheep on successive days while grazing swards of different structures. (Values are means of 4 animals x 2 weeks).

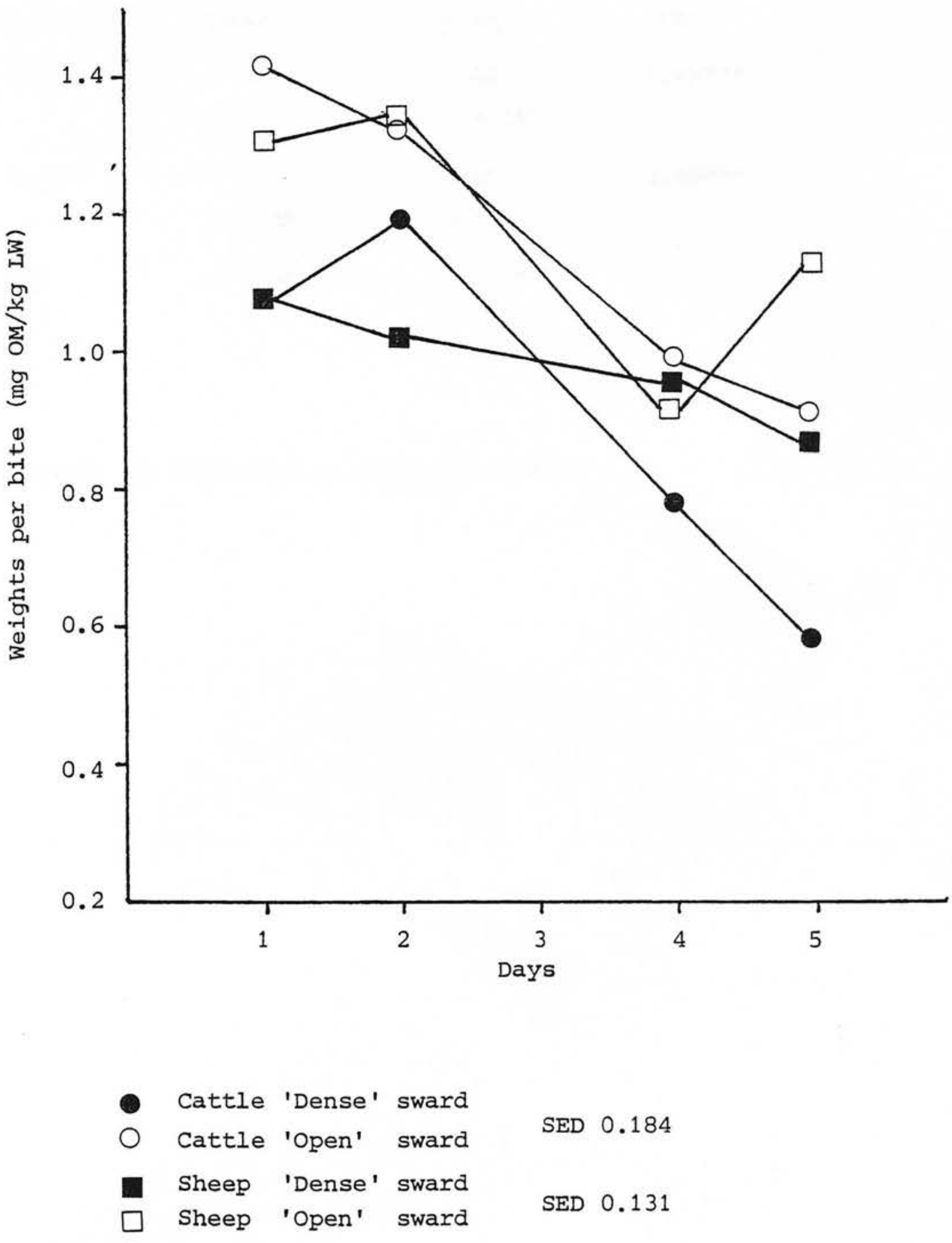


Table E1.7

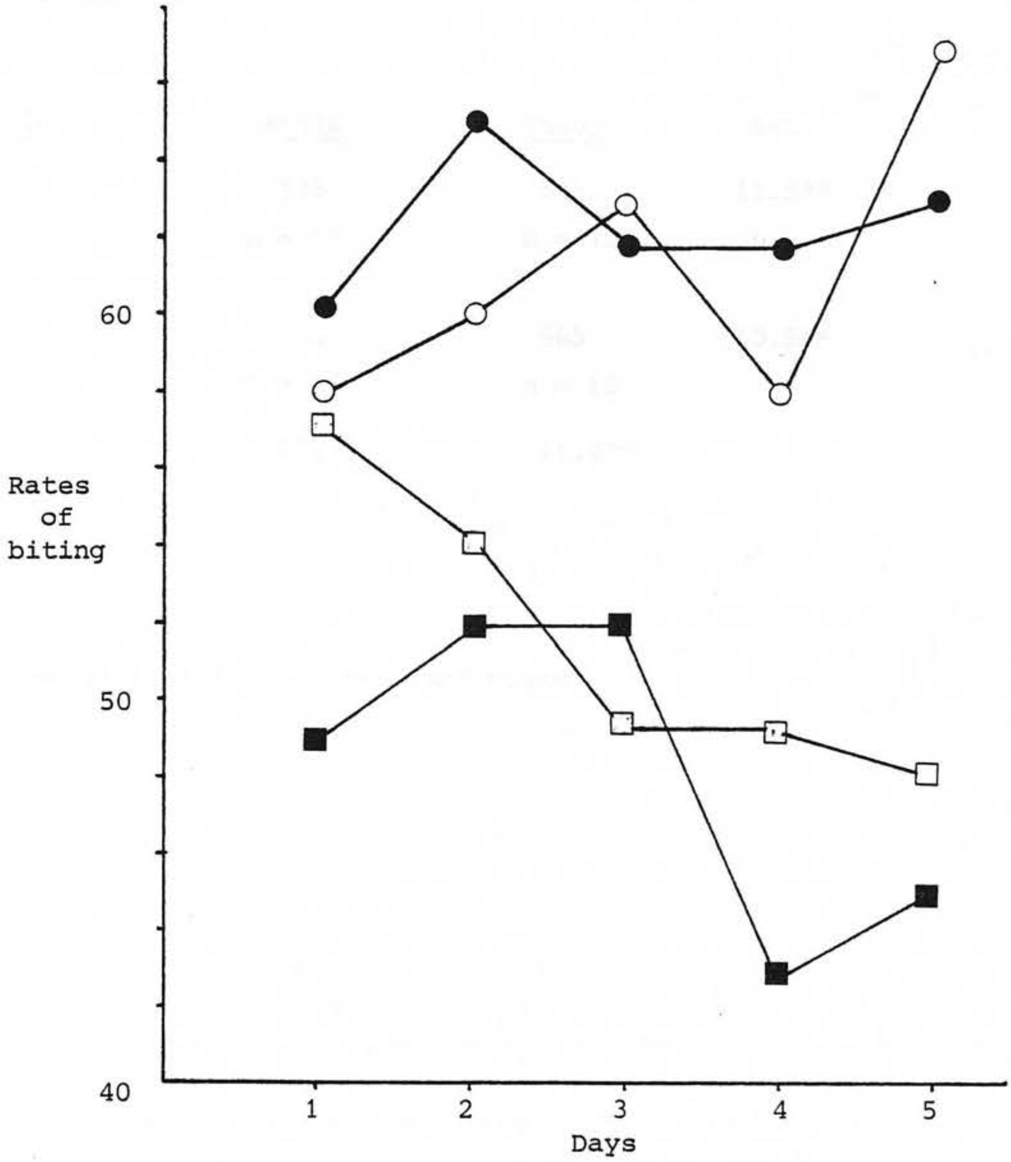
Rates of biting (bites/min) by the cattle and the sheep on the 'dense' and 'open' swards †

Swards	Cattle	Sheep	SED
'Dense'	62	48	1.45***
	n = 35	n = 35	
'Open'	60	52	1.49***
	n = 36	n = 31	
SED	1.44NS	1.50*	

† means of individuals, days and weeks

Figure E1.6

Rates of biting by the cattle and sheep on the 'Dense' and 'Open' swards



● Cattle 'Dense' sward
○ Cattle 'Open' sward
SED 1.44 NS

■ Sheep 'Dense' sward
□ Sheep 'Open' sward
SED 1.50 *

Table E1.8

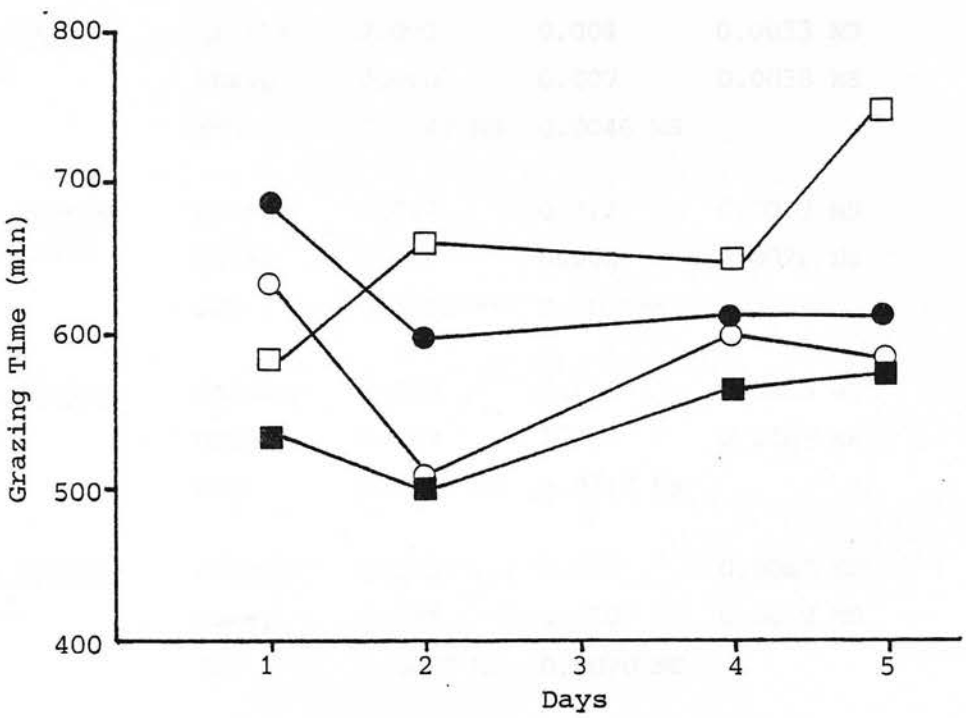
Time spent grazing (min/day) by the cattle and sheep on the two swards

Swards	Cattle	Sheep	SED
'Dense'	625	545	11.5**
	n = 15	n = 12	
'Open'	580	665	10.5**
	n = 16	n = 16	
SED	10.7*	11.4**	

† Means of individuals, days and weeks

Figure E1.7

Grazing times by the cattle and sheep on successive days whilst grazing swards of different structures. (Values are means of 4 animals x 2 weeks. No measurements were made on day 3).



● Cattle 'Dense' sward
○ Cattle 'Open' sward
SED 10.7*

■ Sheep 'Dense' sward
□ Sheep 'Open' sward
SED 11.4**

Table E1.9

The proportions of the major components of the diets of the cattle and sheep grazing the 'dense' and 'open' swards †

Dietary Component		Sward 'Dense'	'Open'	SED
Green grass leaf	Cattle	0.877	0.834	0.0453 NS
	Sheep	0.861	0.905	0.0325 NS
	SED	0.0398 NS	0.0390 NS	
Dead grass leaf	Cattle	0.003	0.004	0.0053 NS
	Sheep	0.010	0.007	0.0038 NS
	SED	0.0047 NS	0.0046 NS	
Green vegetative stem	Cattle	0.017	0.012	0.0037 NS
	Sheep	0.002	0.002	0.0026 NS
	SED	0.0032***	0.0032**	
Green flower stem	Cattle	0.078	0.114	0.0368 NS
	Sheep	0.103	0.065	0.0265 NS
	SED	0.0324 NS	0.0317 NS	
Green flower head	Cattle	0.025	0.035	0.0082 NS
	Sheep	0.024	0.020	0.0059 NS
	SED	0.0072 NS	0.0070 NS	

† Cattle values are means of 15 samples on the 'dense' sward and 16 samples on the 'open' sward. Sheep values are means of 30 samples on both swards.

on the 'dense' sward was 590 mins/day compared with 622 mins/day on the 'open' sward. The full results of the ANOVA are given in Appendix Table E1.9.

Diet composition: The proportions of the major herbage components in the extrusas of the cattle and sheep are given in Table E1.9; other components were negligible. The results of the ANOVAs on the different components are given in Appendix Tables E1.10.1 to E1.10.5. The coefficients of variation, though high, are in line with the results of Van-Dyne and Heady (1965). Differences between the cattle and sheep in the proportions of the components in their diets were generally small with the exception of vegetative and flower stem. Though the interaction of animal species x swards was not significant (Appendix Tables E1.10.1 to E1.10.5) the difference in the amounts of vegetative stem in the animals' diets was compared since the differences were so marked and they were found to be highly significant (Table E1.9). The differences in the amounts of flower stem were found to be non-significant.

Live weight: The mean live weights of the cattle and sheep over the course of the experiment were respectively 570 ± 13.5 kg and 62.3 ± 1.25 kg.

Discussion

Sward conditions

The herbage mass was slightly greater before grazing in the second week than in the first due to the extra week's growth, but the differences were not significant (Table E1.2). Grant, Barthram and Torvell (1981) in a regrowth experiment on the same sward in the previous summer found that irrespective of previous defoliation treatment, similar levels of herbage mass accumulated over a four week regrowth period. This would certainly account for the lack of significant differences in herbage mass between the swards. No tiller counts were made in the present experiment so it is not known if there were differences in tiller numbers between the swards, and though there did appear to be a greater weight of vegetative stem on the 'dense' sward than on the 'open' sward prior to grazing (Table E1.3) the difference was not significant. The 'open' sward was significantly taller than the 'dense' sward overall, and whilst on the 'dense' sward surface height was greater on the cattle than on the sheep plots the situation was reversed on the 'open' sward. The shortness of the herbage on the sheep plots on the 'dense' sward appeared to be due to an uneven application of fertilizer, but this did not seem to be a valid explanation of the low sward height on the cattle plots relative to the sheep plots on the 'open' sward. The measurement technique used is open to some criticism on the grounds that disturbance of the herbage is unavoidable, and that as it is a measure of surface height differences between swards in the amount of flattening by wind might lead to differences in sward height.

There were obvious changes in the structures of the swards as a result of grazing, which are illustrated in Figures E1.3.1 to E1.3.8 and detailed in terms of the weights of the different components in the successive sward horizons in Appendix Tables E1.3.1 to E1.3.4. The most obvious change was the reduction in sward height and mass. The point quadrat data which are illustrated in Figures E1.3.1 to E1.3.8 are given as numbers of contacts from a constant number of points rather than proportions and as such can be used to give an estimation of the density of the swards in each horizon. It also shows the change in density of the different components in different horizons as a result of grazing. The change in sward height seen in the figures probably reflects the reduction due to grazing though it may possible reflect, as pointed out by Spedding and Large (1957), the degree of trampling of the herbage.

Figure E1.8

The sheep and cattle plots on the 'dense' sward after grazing in the first week of the experiment

Sheep plot

Cattle plot

Both the point data and the horizon separations suggest that there was a general increase in dead material in the swards after grazing. In week 2, however, the sheep appeared to remove a large amount of the dead material that was in the upper horizons of the 'dense' sward. This was confirmed by examination of the proportions of dead material in the extrusa samples of the sheep on this plot, and by the observation that the OMD of the sheeps' diet was slightly, but not significantly, lower at this time compared to the previous week. Apart from this the cattle appeared to be less selective than the sheep, consuming more vegetative stem than the sheep (Table E1.9) and more of the stem in the upper horizons (Figures E1.3.1 to E1.3.8 and Appendix Table E1.3.2). None of these differences could be shown to be significant, but they do indicate that even on swards of similar structure cattle and sheep graze in a different manner. The analysis of the variances of the mean sward heights after grazing (Appendix Table E1.5) shows that grazing by the cattle and sheep did produce swards of different appearance (Figure E1.8), with the cattle swards being more uniform in height. It is possible, since the measurement was of surface height, that the effect is due to trampling, but this seems unlikely. The greatest difference between the cattle and sheep plots occurred on the 'dense' sward in week 1, where there was a large difference between the plots in the amounts of flower stem in the sward at the start of the experiment. Results from Barthram (1980) from work carried out on the same swards suggest that sheep avoid layers of the sward containing large amounts of stem material and thus ungrazed areas may become increasingly unattractive to sheep as the sward matures. Large and Spedding (1964) and Morris (1969) found that lambs grazed in a patchy manner, and it is feasible to suppose that a rotational pattern can develop with the animals returning more frequently to shorter previously-grazed areas than to taller ungrazed areas.

Alternatively the patchiness could have been a result of the presence of dung patches from the previous preparatory grazing by sheep. Examination of Figure E1.8 suggests that the patches were too extensive to be entirely due to dung, and there do not appear to be any comparable patches on the cattle plot that might have been due to sheep dung. The potential influence of dung on the herbage utilization of cattle and sheep was investigated further in Experiment 2.

Animal responses

Comparative studies of the ingestive behaviours of sheep and cattle in relation to the structure of the sward appear to be limited to the work of Jamieson and Hodgson (1979b) and Hodgson (1981), though Le Du and Baker (1981) report on a comparison of the digestibilities of the diets selected by cows and sheep. As a consequence of the paucity of comparable experiments with which to discuss the results of this experiment it was necessary to examine the results of experiments that looked at the responses of single animal species to changes in the sward.

The digestibility of the diets selected by both the cattle and sheep did not differ significantly between the swards, nor did it decline significantly as grazing proceeded (Figure E1.4). The sheep selected diets higher in digestibility than the cattle on both swards; a finding consistent with those of Dudzinski and Arnold (1973) and Langlands and Holmes (1978). When the values for the two swards were meaned the sheep had significantly higher diet digestibilities on days 1 and 5 than on other days, while for the cattle day 5 was significantly lower than day 2. Thus while the cattle show very slight evidence for a decline in diet digestibility with time, the sheep do not. The explanation probably lies in the fact that the cattle diet contained more stem than the sheep diet, particularly by the last day of each week which resulted in a decline in the digestibility of the cattle diet.

The sheep on the other hand had a reduced diet digestibility in mid-week which may have been due to an initial lack of selectivity, followed by increased selection for green leaf as the swards were grazed down later in the week. There was still sufficient herbage remaining on the plots to allow selection at the end of a week.

The responses of the cattle and sheep in the weight of herbage taken per bite over the course of the grazing period were similar on both swards, with the weight per bite being significantly lower in the second of the two within-week sub-periods (Table E1.6) when the swards had been partially grazed. The sheep bite weights showed a significant decline with time on the 'dense' sward but not on the 'open' sward, whilst the bite weights of the cattle declined significantly on the 'open' sward but not on the 'dense' sward (Figure E1.5). On a live-weight basis there was no difference between the weights per bite of the cattle and sheep, though Jamieson and Hodgson (1979b) found that lambs had larger intakes per bite than calves. On a $LW^{0.75}$ basis the cattle had significantly ($P < 0.01$) higher intakes per bite than the sheep (4.58 vs 3.29 ± 0.310 mgOM/bite kg $LW^{0.75}$). This finding is similar to that found by Jamieson and Hodgson (1979b). The decline in weight per bite by the cattle over the grazing period is similar to that found by Stobbs (1973a) and to that found for calves and lambs by Jamieson and Hodgson (1979b). The weights per bite of the cattle (g OM/kg LW per bite) are somewhat lower than those given by Hodgson and Jamieson (1981) for lactating cows grazing ryegress swards, but are within the range of bite sizes given by Stobbs (1973a) for cattle grazing tropical swards. The decline in weight per bite with time on a plot is obviously related to the reduction in either herbage mass or herbage height or both, as has been found by other workers (Allden and Whittaker, 1970; Jamieson and Hodgson, 1979b; Hodgson, 1981; Hodgson and Jamieson, 1981). There are however too few data points to regress weight per bite on herbage mass or height.

Previous studies have shown that as weight per bite declines there is generally an increase in either rate of biting or grazing time or both, depending on the particular sward conditions (Allden and Whittaker, 1970; Chacon and Stobbs, 1976; Chacon, Stobbs and Dale, 1978; Jamieson and Hodgson, 1979b). However, though there was a significant sward x animal species x day interaction for rate of biting the regressions showed that there was no consistent change with time in the rate of biting by the cattle on either sward nor was there a significant decline in the rate of biting by the sheep on the 'dense' sward, though the decline on the 'open' sward was significant (Figure E1.6). The rates of biting by the cattle were significantly faster than the sheep on both swards (Table E1.7). The cattle had almost identical rates of biting on both swards while the sheep were significantly slower on the 'dense' sward. This latter observation is in disagreement with results from an earlier study on very similar swards carried out at HFRO (Annual Report 1976) where it was found that rate of biting was slower on the 'open' sward. In this experiment rate of biting by the sheep declined along with a decline in weight per bite, unlike the cattle who appeared to follow the normal pattern and increase or at least hold constant rate of biting while weight per bite declined. The rates of biting by both cattle and sheep were within previously published limits (Allden and Whittaker, 1970; Chacon and Stobbs, 1976; Jamieson and Hodgson, 1979b) but to make comparisons between values obtained from animals grazing very different swards is not a particularly valid exercise.

The third ingestive behaviour parameter, grazing time, appears to be used by grazing animals to modify the effects of rate of intake (weight per bite x rate of biting). Up to a point grazing time will increase as rate of intake declines (Allden and Whittaker, 1970; Chacon and Stobbs, 1976; Jamieson and Hodgson, 1979b), but then grazing time and rate of intake tend to decline in step resulting in a rapid reduction in daily herbage intake (Allden and Whittaker, 1970; Chacon and Stobbs, 1976). In this experiment the cattle did not significantly increase or reduce grazing time on either sward as grazing proceeded and neither did the sheep on the 'dense' sward. On the 'open' sward however the sheep increased grazing time from 575 min/day on the first day to 745 min/day on the fifth day. On this sward both weight per bite and rate of biting declined as grazing proceeded, and the increase in grazing time (Figure E1.7) may be interpreted as an attempt by the sheep to maintain levels of intake. The cattle and sheep responded to the swards in a very different manner (Table E1.8), and the grazing times are high in comparison to other published results (Allden and Whittaker, 1970; Jamieson and Hodgson, 1979b; Baker, Alvarez and Le Du, 1981; Hodgson and Jamieson, 1981). The cattle grazing times are somewhat similar to those found by Chacon and Stobbs (1976) for cattle grazing a tropical sward. It is possible that these values are over-estimates since the animals were troubled to a certain extent by flies, which may have caused a certain amount of head-shaking and thus the accumulation of spurious data. Generally however the traces on the vibracorder charts were extremely distinct with grazing periods well defined, making interpretation relatively easy and reducing the likelihood of overestimation. Using the regression determined by Castle, MacDaid and Watson (1975) for lactating cattle, the predicted mean grazing times for the cattle would be 500 min/day and 513 min/day on the 'dense' and 'open' swards respectively, for lower values than the 625 and 580 min/day actually recorded.

Table E1.10

Daily herbage organic matter intakes calculated from the mean daily weights per bite (mgOM/kgLW), bite rates (bites/min) and grazing times (mins/day) presented as gOM/kgLW/day and kgOM/day. (No measurements were made on the third day)

	Swards							
	'Dense'				'Open'			
	gOM/kgLW/day		kgOM/day		gOM/kgLW/day		kgOM/day	
Day	Cattle	Sheep	Cattle	Sheep	Cattle	Sheep	Cattle	Sheep
1	44.9	28.7	25.2	2.0	52.5	43.8	29.5	3.0
2	46.7	26.3	26.2	1.8	39.5	48.3	22.1	3.3
4	30.2	23.2	16.9	1.6	34.6	29.2	19.4	2.0
5	22.9	22.6	12.9	1.6	34.9	40.4	19.6	2.8
Mean	36.2	25.2	20.3	1.7	40.4	40.4	22.7	2.8
SE	±5.77	±1.42	±3.24	±0.10	±4.19	±4.08	±2.35	±0.28

Unfortunately it was not possible to record daily changes in the swards on to which the changes in the ingestive behaviour could have been regressed, but it appears that the cattle responded to declining herbage mass and declining sward height mainly by a reduction in weight per bite, without corresponding increases in rate of biting and grazing time. The sheep response also involved a reduction in weight per bite, but there was also a decline in rate of biting, particularly on the 'open' sward, and this was compensated for by an increase in grazing time. Some of the differences in the animals' responses compared with other published results may reflect the lower range of sward conditions found in this experiment.

These responses are of some interest when daily herbage intake is estimated from weight per bite, rate of biting and grazing time (Chacon, Stobbs and Sandland, 1976). Table E1.10 gives the estimated herbage organic matter intakes of the cattle and sheep, both as mgOM/kgLW and as kgOM/day. The estimates, particularly for the first three days, appear unrealistically high, and it is logical to assume that one or more of the three parameters must be an over-estimate. Over-estimation of weight per bite can come about by over-estimation of the weight of extrusa collected or by under-estimation of the number of bites taken. The former alternative is very unlikely and in fact, even with the use of throat plugs, recoveries of less than 100% are likely. Under-estimation of the number of bites taken is considered unlikely since the operators are experienced and there were no difficulties in seeing the animals. Possible errors in the 20-bite method have already been discussed as have the possible causes of over-estimation of grazing time. The mean daily intakes (kg OM/day) (Table E1.10) of the cattle on both swards and the sheep on the 'open' swards are much higher than other published values for similar classes of stock

(Langlands, 1968; Hodgson and Milne, 1978; Hodgson and Jamieson, 1981), however the values of the sheep on the 'dense' sward are lower than values found by Hodgson and Milne (1978). If the degree of over-estimation is consistent for both animal species on both swards then the intakes of the sheep on all days on the 'dense' sward and for the cattle on the last day on the same sward would have been very much lower than they appeared to be (Table E1.10). In general, however, measurements of herbage intake are mean values from several animals usually taken over 5 or more days, whereas these are values for individual days with the estimates for grazing time and weight per bite coming from only two animals. The digestibilities of the diets were high throughout the course of the grazing period and it was noticeable that the faeces of the cattle were very liquid, whilst those of the sheep were very soft, suggesting a rapid passage of feed. Also the animals may have suffered a degree of feed restriction immediately prior to the experiment. It may be argued then that these intakes reflect a transient and rare occurrence of over-eating by animals presented with highly digestible and readily accessible herbage. With digestibilities over 0.70 it is unlikely that physical limitations would have restricted intake (Hodgson, 1977) and over such a short time period metabolic controls may have been involved.

The decline in herbage intake as a consequence of the decline in weight per bite as grazing continued is probably due to a reluctance of the animals to graze into horizons of the sward containing large proportions of stem. Barthram (1980) has shown that herbage intakes of sheep may be limited if the animals are forced to graze into the stem and sheath horizons of the sward. The horizons containing appreciable amounts of stem extended 10-15 cm upwards from the ground on both swards, and the animals were having to graze below this level at the end of each week.

Conclusions

The experiment provided useful information on the responses of cattle and sheep to simple changes in sward conditions. The high herbage mass at the start of the experiment was not reduced sufficiently to cause large compensatory changes in ingestive behaviour. The observation that calves were no better than lambs at dealing with long swards (Hodgson, 1981) can be said to be confirmed in this experiment with regard to adult cattle and sheep, though there is some evidence that the distribution of stem within the sward did influence the sheep to a greater extent than the cattle. It appeared that the cattle grazed the sward down by a relatively uniform removal of successive layers, unlike the sheep, which on stemmy swards produced a distinctly patchy pattern of defoliation.

EXPERIMENT 2

The reaction of grazing sheep and cattle to the presence of dung from the same, or the opposite species

Introduction

Animal production per unit area under mixed stocking is generally claimed, for a number of reasons, to be equal to or greater than under single species stocking (Nolan and Connolly, 1977). One of the many reasons put forward to explain the improvement brought about by mixed grazing is that there is sufficient complementarity of grazing activity to allow one or both species to obtain higher nutrient intakes than would be the case under single stocking (Peart, 1963; Van Keuren and Parker, 1967; Dudzinski and Arnold, 1973). This effect is most likely to be seen on those swards where there is the greatest opportunity for diet selection to occur, but on highly productive pastures with high stocking rates the presence of dung and the associated rejected herbage may be considered a circumstance where complementary grazing effects could enable one or more of the grazing species to obtain increased herbage intakes (Nolan, 1981). The influence of dung on herbage use has been illustrated by a number of authors (Marten and Donker, 1964 a & b; Greenhalgh and Reid, 1969; Marsh and Campling, 1970; Wade and Le Du, 1981) but apart from De Rancourt, Nolan and Connolly (1981) and Huber (personal communication) there appear to have been no experimental comparisons of the reaction of sheep and cattle to their own or the opposite species dung.

The responses of the animals to the swards in Experiment 1 might possibly have been influenced by the amount of sheep dung on the sward

Table E2.1

The design of Experiment 2

Treatments	Levels
Blocks	2
Sub-blocks within blocks	2
Plots (current grazers)	2 (Cattle;Sheep)
Sub-plots (previous grazers)	2 (Cattle;Sheep)

The sub-blocks within blocks were grazed consecutively, with each grazing period lasting for 3 days .

as a consequence of the previous preparatory grazing treatments, as was suggested by Wade and Le Du (1981). This experiment was designed therefore to investigate the reactions of grazing cattle and sheep to the dung of the same or the opposite species through sward measurements and measurements on aspects of grazing behaviour, in order that some understanding might be reached of the influence of dung avoidance on herbage utilization. Though the influence of dung from either the same or the opposite species may be of importance under mixed grazing management on sown swards it is unlikely that dung effects would influence the animals' responses under the conditions of Experiment 3.

Materials and Methods

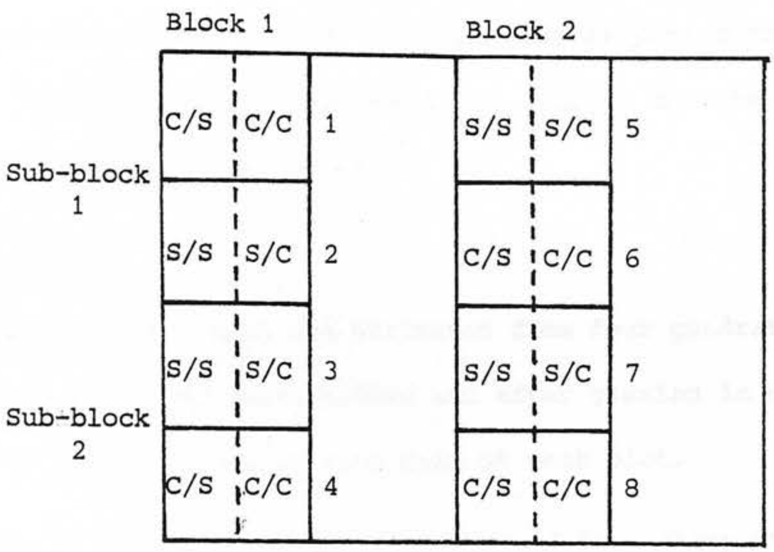
Design and management

The basic design of the experiment is given in Table E2.1. The experiment consisted of two plots within two sub-blocks within two blocks. The four sub-blocks per treatment were grazed consecutively, in four 3-day measurement periods with each period acting as a replicate. The plots were laid out so that half of each plot had previously been grazed by sheep and half by cattle giving the following sub-plots: cattle grazing sub-plots previously grazed by sheep (C/S), cattle grazing sub-plots previously grazed by cattle (C/C), sheep grazing sub-plots previously grazed by sheep (S/S) and sheep grazing sub-plots previously grazed by cattle (S/C).

The plots were 500 m^2 in area and were laid out on the swards used in Experiment 1 as illustrated in Figure E2.1. At the end of Experiment 1 the whole area was cut with a forage harvester to remove residual herbage; 40 kg N/ha as Nitram was applied to the whole area and the sward allowed to regrow for four weeks until the beginning of the experiment.

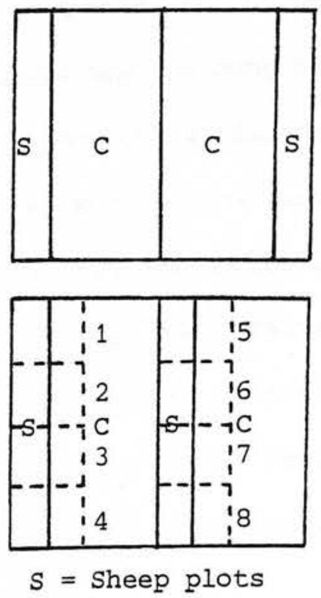
Figure E2.1

The layout of the plots in Experiment 2



C/S = formerly grazed by sheep, currently grazed by cattle
C/C = formerly grazed by cattle, currently grazed by cattle
S/S = formerly grazed by sheep, currently grazed by sheep
S/C = formerly grazed by cattle, currently grazed by sheep

The position of the plots in relation to Experiment 1



S = Sheep plots
C = Cattle plots

Four Hereford x Friesian bullocks and eighteen Blackface wethers grazed their respective plots in succession. To avoid confusing the effects of previous and current dung deposition on the pattern and distribution of grazing all the animals wore faecal collection bags throughout the experiment. All the animals were accustomed to the bags in a two-week preliminary training period during which they grazed on a similar ryegrass sward. During the experimental period the bullocks' bags were emptied at 0830h and 2000h, whilst the sheeps' bags were emptied once a day at 0900h.

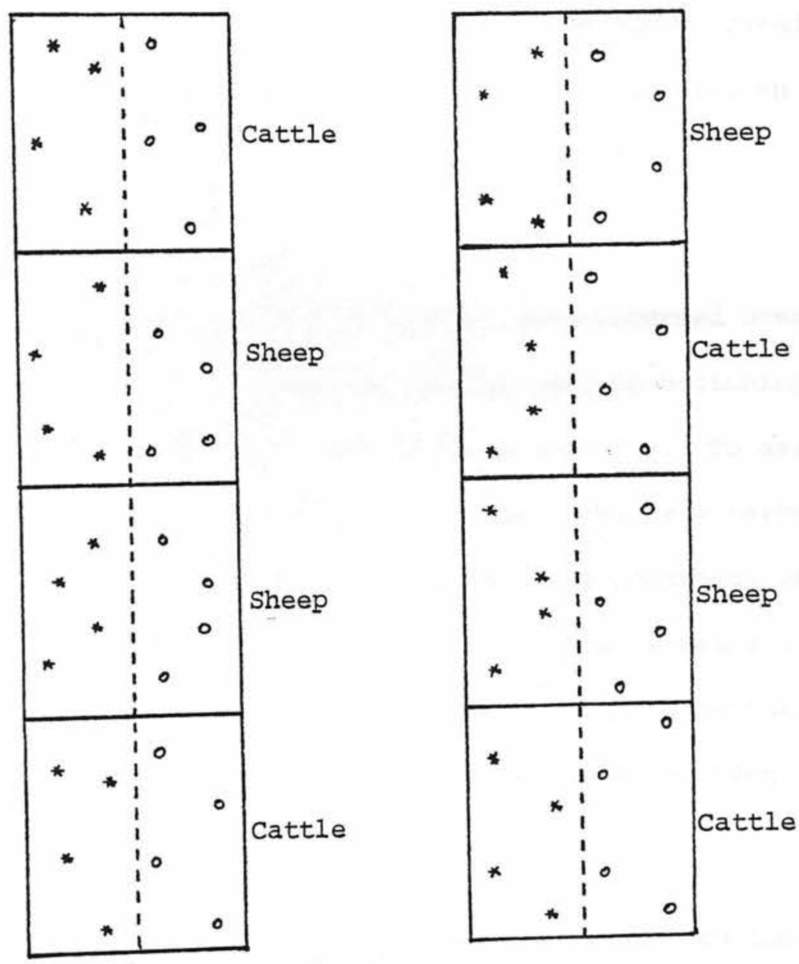
Sward measurements

(1) Herbage mass: Herbage mass was estimated from four quadrats (15 x 122 cm) cut to ground level before and after grazing in each period, two quadrats being cut in each half of each plot.

(2) Fixed transects were laid across four cow and four sheep dung patches from the previous grazing on each plot. The transects were orientated to make allowances for possible slope and wind direction effects on herbage growth. The dung patches were selected to give the distribution illustrated in Figure E2.2, and an attempt was made to choose the largest sheep dung patches and the most uniformly deposited cow dung patches. The sheep dung chosen was always a large non-pelleted patch; a result of the diet quality at the previous grazing. The transects were 2m in length across the cow dung patches and 1.5m in length across the sheep dung patches, the different lengths reflecting the different sizes of dung patch and assumptions about the likely extent of the influence of a patch on the surrounding herbage. Sward surface height was measured along the transects at 2cm intervals at the beginning and end of each period. Extended sward height measurements similar to those used by Hodgson, Tayler and Lonsdale (1971) were also made on the same leaves used for surface height except that measurements were only

Figure E2.2

The distribution† of dung patches across which transects were laid in each plot of Experiment 2



* sheep dung
o cattle dung

† The distribution was determined by the presence of suitable dung patches (see text)

made on single leaves, using a graduated pin to minimise sward disturbance. To enable before-and-after grazing measurements to be made in the same place, a marked string was stretched between the two transect markers during the taking of measurements.

(3) At the start and finish of each period two diagonal transects were laid across each plot so that one crossed the half previously grazed by sheep whilst the other crossed the area previously grazed by cows. Surface height was recorded at 0.5m intervals to give an estimation of the patchiness of grazing within the plots.

Animal measurements

The positions of the animals whilst grazing were recorded every ten minutes for one hour during the major grazing periods beginning at approximately 0600h, 1000h, 1600h and 1900h on each day. To assist recording the positions of the grazing animals the plots were marked out in a grid of 6m squares with coloured stakes. The positions of the animals were then marked on especially prepared charts using a different colour code at each ten minute interval, so that the changes in grazing distribution over the grazing period could be recorded.

Statistical analyses

Transect measurements: Regression analysis was carried out on the measurements of extended sward height after grazing on the dung-patch transects (MULTREG program. Day and Middleton, 1972) and analysis of variance was then carried out on the resulting intercepts and coefficients of slope in a split-split-plot design (EDEX program. Hunter, Patterson and Talbot, 1979).

Animal positions: The distributions of the cattle and sheep within the plots whilst grazing was analysed using a generalised linear modelling program (GLIM. Nelder, 1974). Prior to the analysis the numbers of sheep and cattle recorded as grazing in the separate halves

Table E2.2

The weight of herbage (kg DM/ha) on the plots before and after grazing †

Plots	Pregrazing	Postgrazing
C/S	4788	2656
C/C	4291	2831
S/S	4788	3228
S/C	4506	2871
Mean	4593	2897
± SE	149.3*	

SE for comparison within table ± 284.1 NS

† Values are means of 2 blocks x 2 sub-blocks x 2 quadrats

of the plots at each ten-minute interval were summed within each hour that measurements were made. For the analysis the data from the following grazing periods were used in order that within-day movements within the plots could be examined: mid-day, mid-afternoon and evening for the first two days, and early- and mid-morning on the third day.

Results

Sward measurements

Herbage mass: The weights of herbage in the plots before and after grazing are given in Table E2.2. The values presented are the plot means before and after grazing. Herbage mass was significantly lower after grazing than before ($P < 0.01$; Table E2.2) and was greater in sub-block 1 than in sub-block 2 (4077 vs 3413; $P < 0.01$). The full ANOVA results are given in Appendix Table E2.1. There were no significant differences between treatments.

Sward height: The surface heights of the swards in the plots before grazing are given in Table E2.3. The effects of blocks, sub-blocks and previous grazers were all significant ($P < 0.001$) as was the interaction between previous and current grazers ($P < 0.001$). The complete ANOVA table is presented in Appendix Table E2.2. The halves of plots previously grazed by the cattle were significantly ($P < 0.001$) taller than the halves previously grazed by the sheep.

Transect measurements

Prior to regression analysis on the measurements of extended sward height along the transects laid across the dung patches, the transects across cattle dung were reduced to 70cm from the edges of the dung as it was apparent that when the full transect length was used, the end measurements were in some cases being distorted by the presence of nearby dung patches. Thus transect lengths across cattle

Table E2.3

The surface height of the swards before grazing for the treatments C/S, C/C, S/S and S/C

	Previous grazers			
Current grazers	Cattle	Sheep	Mean	SE
Cattle	20.0	17.3	18.7	± 0.26 NS
Sheep	18.0	18.0	18.0	
Mean	19.0	17.7		
± SE	± 0.26***			

SE for comparisons within table 0.37***

and sheep dung patches were the same. The two halves of each transect were analysed separately so as to give 32 half transects for each of the sub-plots: C/S, C/C, S/S and S/C. The proportion of transects in each of the sub-plots that had significant ($P < 0.05$) negative slopes is given in Table E2.4, as an indication of the extent of avoidance of the dung within each sub-plot.

Table E2.4

The proportions of transects across cattle and sheep dung pats, in areas grazed by the same or the opposite species, that demonstrated significant negative regressions ($P < 0.05$). n = 32.

	Previous grazers	
Current grazers	Cattle	Sheep
Cattle	0.84	0.34
Sheep	0.56	0.56

The intercepts and slopes of the regression equations were subjected to analysis of variance to examine in more detail differences in response to the herbage around the dung of the same or the opposite species, by the cattle and sheep. Table E2.5 gives the overall mean intercept and slope for each sub-plot. The results of the analysis showed that the current grazer x previous grazer interaction was significant for intercepts. No other effects were significant, nor were any of the effects significant in the analysis of the slopes. The full results of the two ANOVAS are given in Appendix Tables E2.3 and E2.4. The combination of the results of the analyses of the intercepts and slope coefficients suggest that the cattle removed less herbage from around cattle dung than from around sheep dung whilst sheep removed slightly more herbage from around cattle dung than from around sheep dung.

The patterns of defoliation on each of the plots were compared by

Table E2.5

The mean height (cm) of the intercepts and the mean slope coefficients from the regressions of extended sward height on the distance from the edge of the dung patches for the treatments C/C, C/S, S/S and S/C †

Intercepts

Current grazers	Previous grazers: Cattle	Previous grazers: Sheep	± SE[a]
Cattle	24.0	19.0	
			0.82*
Sheep	21.2	24.3	
± SE[b]	0.63*		

Slopes

Current grazers	Previous grazers: Cattle	Previous grazers: Sheep	± SE[a]
Cattle	- 0.21	- 0.10	
			0.030 NS
Sheep	- 0.14	- 0.12	
± SE[b]	0.024 NS		

a = SE for comparisons within current grazers
b = SE for comparisons within previous grazers

† values are the means of 2 half-transects x 2 transects x 2 sub-blocks x 2 blocks

analysing the variances of the mean sward heights using an additive model as described in Experiment 1. The results are given in Appendix Table E2.5. The effects of blocks, sub-blocks and current grazers were all significant, and the variances were greater on the sheep than on the cattle plots indicating that the pattern of defoliation by the sheep resulted in a patchy sward independent of the dung of the previous grazing species.

Animal measurements

The result of the analysis of the positions of the animals whilst grazing relative to the halves of the plots previously grazed by the same or the opposite species is given in Appendix Table E2.6. There were significant ($P < 0.05$) differences between individual measurements within the three-day measurement period, with a significant ($P < 0.05$) overall linear time effect. The slope of the linear effect was negative showing that by the end of each three day measurement period the animals were grazing more frequently on the half of the plot previously grazed by the opposite species. There was no improvement to the fit of the model when a quadratic term for time was fitted. The proportions of the animals grazing areas previously grazed by the same species at different times of day over the three days of each measurement period are given in Appendix Table E2.7.

Discussion

The size of the plots, the numbers of animals and the duration of the grazing periods were chosen in an attempt to obtain a rapid removal of the herbage whilst preventing the overgrazing of initially rejected herbage around dung pats as a result of too high a grazing pressure. The numbers of animals were determined by the number of faecal collection harnesses available for cattle, and the sheep were balanced to the numbers of bullocks on the basis of the results of

Experiment 1 in order to equalise grazing pressures between treatments as far as possible. The ratio of 4.5 wethers to 1 bullock appears to have been quite satisfactory as indicated by the relatively similar amounts of herbage removed during grazing (Table E2.2).

Prior to grazing of plots 1 and 2 (Figure E2.1) only sward surface height measurements were made on both the transects laid across dung pats and the transects laid diagonally across the plots. However subsequent to grazing it was felt that because of the amount of trampling, sward surface height was not an appropriate measurement to describe the degree of removal of herbage from around the dung patches, so subsequently both surface and extended height measurements were made on transects laid across dung pats.

Analysis of the undisturbed surface heights of the herbage along the transects across the dung patches gave a lower proportion of significant negative regressions compared to the analyses based on extended height. This probably reflected a trampling effect on estimates of surface height, so extended sward heights were used in subsequent analyses. The use of the quadratic term did not increase the number of significant negative regressions nor did it consistently improve the fits of the regressions, so the linear term was used to describe the relationship between sward height and distance from the edge of the dung pat. However, it is recognised that the relationship is biologically more likely to be curvilinear than rectilinear. The heights of the intercepts together with the slopes of the regressions indicate that the limits of the rejected herbage were more clearly defined around cattle dung pats than around sheep dung pats when grazed by cattle, whilst there was less distinct avoidance of herbage around both cattle and sheep dung when grazed by sheep.

The progressive movements of the animals from the half of the plot previously grazed by the same species to the half of the plot previously grazed by the opposite species was more marked in the cattle than the sheep. The implication of this movement with time is that the animals started by grazing areas previously grazed by their own species, but then progressively spent more time grazing areas previously grazed by the opposite species. It is possible that this may simply be due to differences in the structure of the two halves of the plots in view of the differences in the herbage heights. This, however, does imply differences between the cattle and sheep in their responses to swards of different structure that were not apparent in Experiment 1, and it seems unlikely that the differences in sward height were sufficient to influence the opportunity for selection within the sward canopy in either the cattle or the sheep. Whatever the reason for animals concentrating grazing on the half previously grazed by the same species early in the 3-day measurement period, it is suggested that as the herbage was grazed down the increase in the amount of contaminated and thus unacceptable herbage on the half of the plot previously grazed by the same species caused the animals to spend an increasing proportion of time grazing the half of the plot previously grazed by the opposite species. The fact that the trend was more marked in the cattle than the sheep reflects the difference between the two species in their tolerance for herbage contaminated by the dung of their own species as shown by the results of the regression analyses (Tables E2.4 and E2.5). The results of the analysis of the sward surface heights before grazing show that the sub-plots previously grazed by sheep were shorter than those previously grazed by cattle, (Table E2.3), presumably as a result of a greater influence of cattle dung and urine, even though both swards had been similarly fertilized to try and avoid just such an effect. The fact that the greatest difference should be found in the sub-plots previously grazed by sheep and about to be grazed by cattle is hard to explain, especially since the plots were allocated at random.

The pattern of defoliation by the sheep led to a more patchy sward irrespective of previous grazing species , but the differences due to blocks and sub-blocks were even larger, suggesting that differences in the sward structure influenced the degree of variability. These results confirm the observation in Experiment 1 that the sward surface is more varied in height after grazing by sheep than by cattle. Huber (personal communication) found that when cattle are forced to graze dung patch herbage they do so from the edges rather than the top, whereas the opposite is the case in sheep. This would tend to produce regressions with higher intercepts and steeper slopes on cattle-grazed than on sheep-grazed swards, in agreement with the results of the current study (Table E2.5). De Rancourt et al (1980) found that sheep 'preferred' the high grass around cattle dung when compared to cattle. They did not examine the influence of sheep dung on cattle or sheep 'preferences', but their results suggest that as the amount of contaminated herbage increased, the sheep increasingly avoided herbage around cattle dung. Huber (personal communication) also found, as in the present experiment, that sheep rejected herbage around their own dung, a finding not in agreement with that reported by Arnold and Dudzinski (1978).

Conclusions

The two techniques used to examine the responses of the animals to their own or the opposite species dung were complementary, the measurement of the movements of the animals from one half of the plot to the other being explained by the results of the regression analyses of the extended sward heights along the transects laid across the dung patches.

The results of this experiment show that cattle are more sensitive than sheep to the presence of their own dung. Cattle were relatively insensitive to sheep dung whilst sheep rejected herbage around cattle and sheep dung equally. As a consequence therefore the wastage of herbage around cattle dung may be less under mixed stocking than under single species grazing, but because sheep reject herbage fouled by their own species and cattle equally (Table E2.4) the advantages of mixed grazing appear to be biased in favour of the sheep.

EXPERIMENT 3

Comparative aspects of the ingestive behaviour and diet selection of cattle and sheep grazing together on a range of indigenous grass and grass-heath hill communities.

Introduction

Recent changes in management systems, such as the two-pasture system, that make better use of the seasonal growth cycle of hill vegetation have been described by Eadie, Armstrong and Maxwell (1973) and Eadie, Maxwell, Kerr and Currie (1973). However the principles were developed on a limited range of vegetation types and there is a need to carry out further studies into the potential of different indigenous hill communities to provide adequate nutrition to grazing animals (Eadie, 1981). Grant and Hodgson (1980) described some of the background information required before appropriate managerial decisions can be made for particular hill conditions. The information required includes knowledge of the potential nutrient intakes of the grazing animals on different swards and includes an assessment of the importance of different plant communities to freely grazing animals. Grant and Hodgson (1980) include details of the limited information on these aspects which is already available, but is however almost exclusively limited to sheep. Though the role of cattle in true hill, as opposed to upland, situations appears to be limited (Cunningham and Smith, 1977; Eadie, 1981) there is some evidence that cattle may improve grazing conditions for sheep (Peart, 1963).

The experiment described here was carried out to compare the ingestive behaviours of cattle and sheep grazing together on a range of indigenous hill grass and grass heath communities and to examine the degree of competitiveness or complementarity shown by the two species in the diets they selected, in relation to detailed measurements of the botanical and morphological composition of the swards.

Materials and Methods

Experimental design

The grass and grass heath communities studied were *Agrostis-Festuca* dominant, *Nardus stricta* dominant and *Molinia caerulea* dominant communities and a perennial ryegrass sward. The ryegrass sward was included in the experiment to act as a reference sward, and was situated on the Hill Farming Research Organisation's research station at Glensaugh, Kincardineshire (latitude 56°54'N, longitude 2°32'W). The other communities were in remote locations between 30 and 100 miles from the Organisation's Headquarters, on land rented from the Forestry Commission and were without any of the normal facilities such as piped water or electricity. These considerations influenced the design of the experiment and the choice of procedures.

Because the communities were so widely spaced and relatively remote a single group of experimental animals was used, as this had the advantage of removing the problems of keeping separate groups of fistulated animals on each community and also reduced the amount of between-animal variation. The animals travelled from community to community in accordance with a timetable of movements covering three complete annual cycles of growth, and designed so that each community was grazed on each of four occasions between early spring and late autumn. It was not possible to graze all the communities in any one year, and since the *Molinia* community was not available

Table E3.1

Periods of measurement on the communities in 1978, 1979 and 1980

Months		Rg	Ns	A-F	Mc
			Swards		
May	E			1979	
	M				
	L	1978	1979		
June	E				
	M				1979
	L		1978		
July	E	1979		1978	1980
	M				
	L				
August	E				
	M				
	L				1979
September	E				
	M				1980
	L			1979	
October	E		1978		
	M				
	L		1979	1978	

Rg = Ryegrass, NS = Nardus, A-F = Agrostis-Festuca

Mc = Molinia, E = Early, M = Mid, L = Late.

until 1979, the timetable was arranged so that the *Agrostis-Festuca* and *Nardus* swards were grazed twice in 1978 and twice in 1979, whilst the *Molinia* site was grazed twice in 1979 and twice in 1980. The perennial ryegrass sward was only grazed once in 1978 and once in 1979. Periods of grazing were chosen to coincide as far as possible with early spring growth, mid-season maturity, late season and autumnal degeneration. Table E3.1 gives the communities and seasons when experimental grazing took place.

On each community two adjoining plots were fenced off, each approximately 4 ha in area. One of each of the pairs of plots was used as a preliminary 'run-in' plot which allowed the animals to familiarise themselves with the vegetation prior to being moved on to the 'measurement' plots. 'Run-in' and 'measurement' plots remained the same throughout the duration of the experiment. The plots on the ryegrass sward were smaller than those on the indigenous communities being only 1 ha in area.

Locations and descriptions of the communities

The location of the ryegrass sward has already been mentioned. The actual plots are situated on a south-east facing slope at an altitude of 150m. The soil is a brown forest soil, of the Strichen Association, and the mean annual rainfall is 991 mm (35 year mean, 1916-1950). The sward consisted primarily of *Lolium perenne* with some white clover (*Trifolium repens*) and a variety of weed grasses and dicotyledenous species.

The *Agrostis-Festuca* community is situated on the southern slopes of the Cleish Hills in Fife (latitude 56°N, longitude 3°29'W), at an altitude of 225m. The soil is a Darleithian brown earth overlying a basaltic intrusion. The mean annual rainfall is 1013 mm (35 year mean 1916-1950, Roscobie Reservoir, Fife). The vegetation prior to the experiment was a type intermediate between Festuca-Agrostis type 5 and Deschampsia-Festuca-Agrostis type 8 (King and Nicholson, 1964).

The Nardus community lies some 2 miles north-east of the Agrostis-Festuca sward (latitude 56°9'N, longitude 3°28'W) at an altitude of 290m. The soil is a poorly drained peaty gley of the Giffnock series and the mean annual rainfall is 1100 mm (35 year mean 1916-1950). The vegetation is a Nardus-Festuca-Deschampsia type 2 (King and Nicholson, 1964).

The Molinia community lies on a north-east facing slope beside the, now dismantled, Riccarton Junction railway station (latitude 55°13'N, longitude 2°42'W) at an altitude between 259m and 290m. The soil is a poorly drained peaty gley of the Alemoor series. The mean annual rainfall (35 year mean 1916-1950 at Wauchope, Borders District) is 904 mm. The vegetation is a Molinia-Festuca-Deschampsia type 1 (King and Nicholson, 1964) with quantities of Juncus effusus and Juncus articulatus in a series of old ditches that run diagonally across the slope.

The communities at various times of year are illustrated in Appendix E3.

General management

Swards

The relatively underutilized state of the three main communities required a programme of controlled grazing in order to produce swards more representative of those commonly found on hill farms throughout Scotland. The Agrostis-Festuca community needed an overall removal of herbage so that plots were heavily grazed by cattle between the first and second grazings and after the second grazing in 1978. These first two grazings aimed to remove between 40% and 50% of the herbage. Subsequent grazings over the winter of 1978-1979, by sheep, and in the summer of 1979, between experimental periods by cattle, attempted to maintain the swards in a "typical" state. On the Nardus community an overall removal of 30% of the herbage was required, but heavy cattle grazing was not desirable in case it led to a breakdown of the characteristic tussock-intertussock mosaic and so most of the grazing was carried out by wethers between experimental periods. However some cattle grazing was carried out specifically to remove some of the tussock herbage, but at low stocking rates (2.5 animals/ha). The Molinia community was burnt in the spring of 1978 and was then grazed by both cattle and sheep over the rest of the year to prevent a build up of Molinia litter. No maintenance grazings were carried out on the community between experimental periods in either 1979 or 1980, though sheep grazed the plots over the 1979-1980 winter months.

Grazing during measurement periods on all communities was light, no more than 10% of current season's growth being removed, to allow the animals maximum opportunity for diet selection.

Animals

Eleven cows were used throughout the experiment of which four were fitted with oesophageal fistulae. In 1978 four non-fistulated and two fistulated cows were Hereford x Friesian with the remainder being Blue-Grey (Galloway x White Shorthorn). In 1979 one of the fistulated Hereford x Friesian cows was replaced by a fistulated Blue-Grey, and in 1980 one of the non-fistulated Blue-Greys was replaced by another Blue-Grey cow. The sheep used were all Blackface ewes of which in 1978 six were oesophageal

Table E3.2

The numbers and breeds of the animals used in each year of Experiment 3

	1978	1979	1980
Cows	4 H x F NF	4 H x F NF	4 H x F NF
	2 H x F OF	1 H x F OF	1 H x F OF
	3 B - G NF	3 B - G NF	3 B - G NF
	2 B - G OF	3 B - G OF	3 B - G OF
Sheep	10 NF	9 NF	9 NF
	6 OF	4 OF	4 OF*

* 2 OF ewes replaced by 2 OF wethers in the second period of the experiment

H x F = Hereford x Friesian
B - G = Blue-Grey
NF = Non-fistulated
OF = Oesophageal-fistulated

All cows and sheep were mature, non-pregnant and non-lactating.

All the sheep were Blackface ewes.

fistulates and ten were entire. In 1979 the numbers were reduced to nine non-fistulated and four oesophageal fistulates. In 1980 the same number were used as in 1979 though during the second Molinia grazing the deaths earlier of two fistulated ewes necessitated their replacement with two similarly experienced fistulated wethers. All the cows and sheep were mature, non-pregnant and non-lactating throughout the course of the experiment. Table E3.2 indicates the numbers and breeds of the animals used in each of the three years.

All the fistulated cows were prepared in 1976. Three of the fistulated sheep were prepared in 1977; two more were prepared in 1978 and a further three in 1979.

Animal management

All the cattle and sheep had prior experience of similar swards and sampling procedures to those to which they were exposed during the course of the experiment. Replacement fistulated sheep ran with the flock for some weeks prior to being used. To ensure that the animals had a period of acclimatization on each sward prior to the taking of measurements the animals grazed the 'run-in' plots for six days prior to the five day measurement period. This also allowed for the development of a stable pattern of excretion of the inert marker used for the estimation of faecal output. Details of routine veterinary treatment are given in Appendix E3.

The cattle were overwintered indoors using the facilities available at the Organisation's Headquarters. Fistulated sheep were overwintered indoors whilst non-fistulated sheep were overwintered outside also at Headquarters.

Measurements

The following series of sward and animal measurements were made on the measurement plots only.

Sward measurements

Herbage mass: Herbage mass was determined on the ryegrass, *Agrostis-Festuca* and *Molinia* 'measurement' plots by the same technique as described in Experiment 1 except that 12 quadrats were cut per plot. On the *Nardus* sward the technique used was somewhat different due to the mosaic of tussock and intertussock vegetation. Three representative turves each of tussock, intermediate and intertussock were dug from the sward and their areas measured prior to being harvested in 3 cm horizons. The individual horizons from each turf were frozen and stored at -20°C for later separation into botanical and morphological components. After separation the individual components were oven-dried at 80°C and weighed. The total weight of components from all the turves was used to determine herbage mass after necessary conversion of DM per turf area to kg DM/ha.

Sward structure and botanical composition: The composition of the sward was measured as described in Experiment 1, using a point quadrat to determine the vertical distribution of components. Twelve randomly selected sampling sites were used on all communities and sampling was continued until 100 contacts had been recorded at each sampling site. All contacts were recorded as the needle passed through the sward. Each contact was identified in terms of species, morphological unit and whether live or dead. Mean sward height was estimated from the first contacts and the data from all contacts was set out graphically in 3 cm horizons as described by Spedding and Large (1957) for the following sward components: total green, total grass leaf, total stem, total dicots and total dead. The botanical composition of the sward was expressed as percentage specific frequency (PSF) for the following live sward components: total herbage, total grass leaf, broad grass leaf, fine grass leaf, total grass stem, grass vegetative stem, grass flower stem and flower head, dicots, Juncus species, miscellaneous species (mainly Carex and Luzula), and for total dead. The grass species that make up the component's broad grass and fine grass are given in Appendix Table E3.1. The PSF for any individual component is the number of contacts made against that component expressed as a proportion of total contacts. The botanical composition of each sward was also determined from separations of snip samples cut with each of the twelve quadrats cut during herbage mass estimation. Each snip sample, roughly 5% of the area of the quadrat cut at right angles to the mid point of the long axis, was separated individually according to species, morphological unit and whether live or dead, before being oven-dried at 80°C for 36h and weighed. Each fraction was calculated as weight per respective quadrat before conversion to weight (kg DM) per hectare.

Animal measurements

Live weight: Since weigh crates were not available on any of the sites except the perennial ryegrass site the animals were weighed at the first opportunity before and after the completion of a grazing period; generally weighings were carried out while the animals were in transit to or from the Molinia community, and the Agrostis-Festuca and Nardus sites. No weighings were carried out between grazing periods on the Agrostis-Festuca followed by the Nardus site or vice versa. Thus weighings were seldom at the same time of day and the extent of gut-fill could vary markedly. In calculations involving the live weight of the animals a mean value was used determined from the total weighings over each year.

Width of mouthparts: In order to provide some information that might help explain differences in the response of cattle and sheep to different sward conditions, measurements were made using calipers across the spread of the incisors of all the animals in 1980.

Intake: Herbage intake was measured by the techniques described by Hodgson and Rodriguez (1970); Rodriguez (1973) and Jamieson (1975). Faecal output was estimated using the chromic oxide dilution technique in which pellets of paper impregnated with chromium sesquioxide (Cr_2O_3) are given to non-fistulated cattle and sheep (Corbett, Greenhalgh and Macdonald, 1958). The cows and sheep received pellets of 10g and 1g of paper containing 2.4g and 0.24g Cr_2O_3 respectively each day for twelve days with dosing occurring at 08.30h and 15.30h. Samples of the pellets were taken daily in each experimental period to determine the actual amount of Cr_2O_3 administered daily.

On the last five days of each experimental period, during the time that the animals grazed the measurement plots, faecal samples were collected from the rectum of each animal at the time of dosing. Each day's collection of faecal samples were frozen with solid carbon dioxide and stored at -20°C until the end of the period. The samples were then thawed and individual animal samples bulked and mixed thoroughly before sub-samples were taken for freeze drying. When dry the samples were ground through a 0.4 mm screen in a Christy-Norris mill. Estimates of Cr_2O_3 concentrations were than made, using a modification of the procedure outlined by Williams, David and Iismaa (1962) and an automated colorimetric determination of chromium using calcium chloride. Ash was determined on the dried, ground samples in order to express faecal output in terms of organic matter.

Extrusa samples were collected on the first, third and fifth days of each measurement week on all of the sites, using the procedures described in Experiment 1. The samples of extrusa once collected were frozen immediately with solid carbon dioxide before storage at $-20^{\circ}C$ until they could be analysed for digestibility and diet composition. When required for analysis the samples were broken up while still frozen and sub-sampled with two thirds being taken for freeze drying, grinding and subsequent in vitro digestion. The other third was used for the determination of the diet selected by the animals. Diet digestibility was determined by in vitro digestion (Alexander and McGowan, 1966), though the reference standards were obtained from herbage collected from similar communities and fed frozen to sheep to appetite (Armstrong and Common, 1981). Once diet digestibility and faecal output had been determined herbage intake was calculated from the following equation :

$$\text{Feed intake} = \text{faecal output} \times \frac{100}{100 - \text{Digestibility}}$$

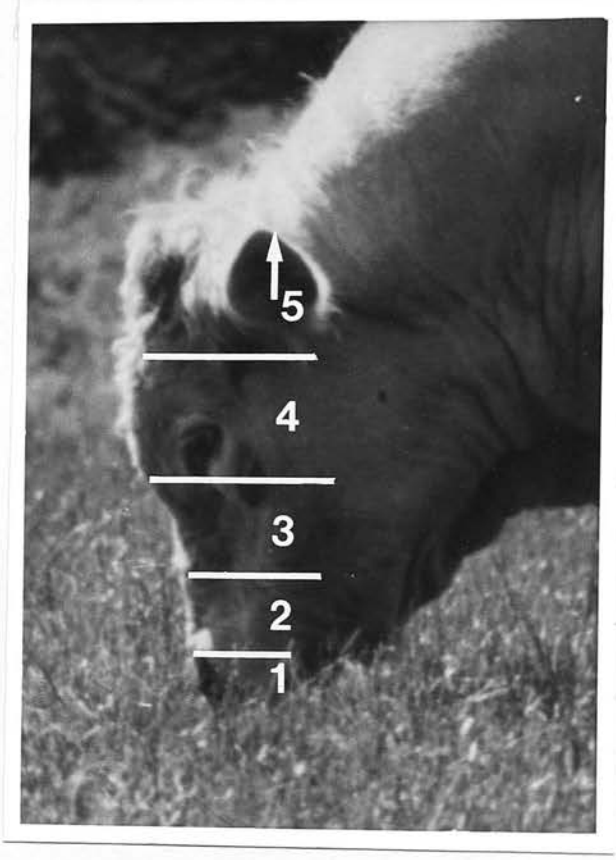
Weight per bite: The weight of herbage taken per bite was determined as described in Experiment 1. Intake per bite was determined indirectly, for non-fistulated animals from estimates of daily herbage intake and total daily bites using the equation:

$$I/B = \frac{HI}{RB \times GT}$$

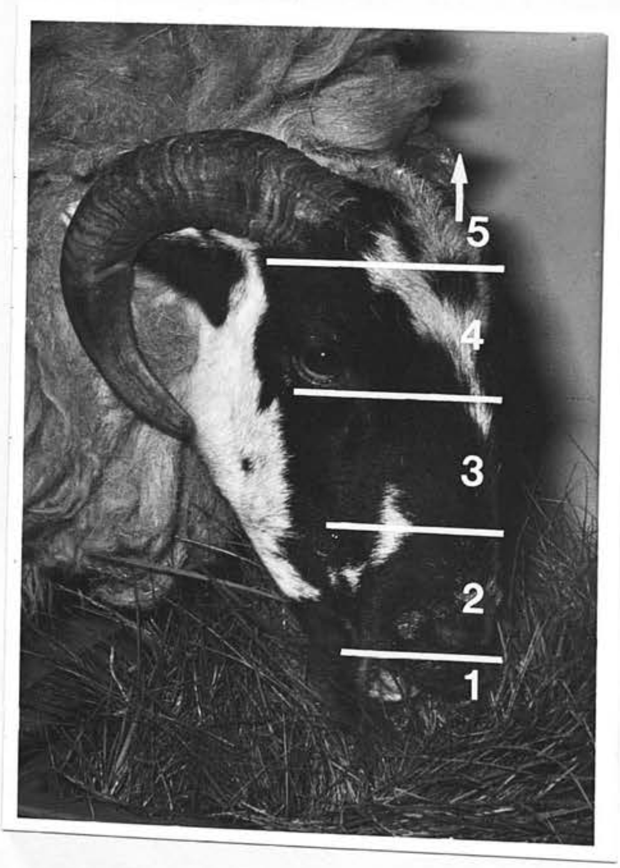
where I/B = intake per bite; HI = mean daily herbage intake; RB = rate of biting and GT = grazing time.

Figure E3.1

Reference points for determining head depth



Cattle



Sheep

Rate of biting: Rate of biting was determined on all animals over four days during the measurement week using the 20-bite technique as described in Experiment 1.

Grazing time: Grazing time was determined, using vibracorders, on five individuals of each species over four days of each measurement period in 1978 and 1980. In 1979 only four individuals of each species were used. The vibracorder charts were changed each morning at dosing time.

Depth of grazing: In order to determine the sward horizons in which grazing was concentrated, estimates were made of the depth to which animals inserted their heads whilst grazing the swards. The measurements were taken during rate of biting recording. The depth of insertion was measured on an arbitrary scale of 1-5 inclusive (Figure E3.1). Thus if the animal's head was obscured by the sward up to the level of the eye it was recorded as being at 3 on the head-depth scale. The same scale applied to both sheep and cows except that in the cows the division between points 4 and 5 corresponded to the base of the ears rather than the horns. The actual distances from the tip of the muzzle to the reference points in the cattle and sheep are given in Table E3.3. Prior to analysis, the records of depths of grazing of the cattle and sheep on the 5-point scale were condensed, since head depths of 2 in the cattle and 3 in the sheep when measured were both around 16.5 cm (Table E3.3) giving a convenient measure of the depth of insertion of the head into the sward from which comparisons could be drawn.

Diet selection: The diet selected by the grazing sheep and cows was estimated from samples of extrusa collected by the oesophageal fistulates. The sub-samples remaining after the samples had been

Table E3.3

Distances (cm) from the tip of the muzzle to the reference points for determining depth of head insertion into the sward, for both cattle and sheep.

	Cattle	Sheep
Muzzle to -		
reference point 1	6.2	3.4
reference point 2	16.5	10.0
reference point 3	26.7	16.6
reference point 4	42.4	22.7
reference point 5	42.4+	22.7+

broken up and sub-divided into samples for freeze drying and samples for botanical analysis were thawed in trays with a little water. After thorough mixing of the thawed material three sub-samples each sufficient to lightly cover the bottom of a 10 cm diameter petri dish were taken, one for each of three regular, trained observers. These were then examined under zoom stereo microscopes (Olympus SZIII) at a magnification of x 7 and the herbage fragments identified, where they lay under the intersections of a gridded eyepiece, until 100 identifications had been made per petri dish (Corbett, 1978). Identifications were carried out to species level on leaf material except for sedges, rushes and mosses. Grass floral parts and flower and vegetative stems were identified where possible to species. Dead material was identified as such.

<u>Selection ratios</u>: Selection ratios were calculated as the ratio of the proportion of a particular component in the diet to the proportion of the same component in the sward. A ratio of 1.0 means that a component occurs in the diet as frequently as it does in the sward, and the higher the ratio the greater the degree of concentration of that particular component in the animals' diet. Conversely the lower the ratio the greater the avoidance of that component.

<u>The length of herbage removed during grazing</u>: Measurements of the length of herbage (mainly leaf and stem) removed during grazing were made in 1979 on all the swards except the May *Agrostis-Festuca* sward. For completeness measurements were made on this sward in July 1980. Two small plots were fenced off on representative areas of each 'measurement' area, one (6m x 6m) to be grazed by cattle and the other (6m x 3m) to be grazed by sheep. Six transects were placed at random within each plot; in the larger plots the transect length was 1.5m whilst in the smaller plots it was 1m. Using a vertical point quadrat measurements of the surface height of the sward were made at 5 cm intervals along each transect. Measurements of extended height were also made on each of the components 'hit' in the surface height measurement by extending the components to full length up a graduated needle, in much the same manner as described by Hodgson *et al* (1971). Measurements were made on both green leaf and flower stem. Pairs of animals were then allowed to graze the plots for short periods of up to 15 to 20 minutes. Extended height measurements were then made on up to 200 grazed leaves in any grazed patches that occurred along the transects. The length of leaf or stem removed was then calculated as the difference between the pre- and post-grazing measurements.

All the measurements were made in the week following the main measurement period, using fistulated animals as they were more amenable to handling. Prior to these measurements all the animals concerned had undergone some training in small pens, but it was recognised that the sheep were less willing to graze particularly if other animals from the flock were within view.

Statistical analyses

Most data collected from animal measurements were subjected to analysis of variance after any necessary preliminary calculations or transformations. Split-plot and split-split-plot factorial designs were used with animal species as the main plot effects and swards as sub-plot effects. The effect of fistulation was treated as a main plot wherever necessary whilst days were assigned to sub-sub-plots. The analyses were carried out using the EDEX program (Hunter, Patterson and Talbot, 1979) which enabled data sets with unequal frequencies to be analysed, as it was not feasible to calculate the missing values. In all analyses the first error term contained the effect of individual animals-within-animal species, together with the relevant interaction terms. Where applicable Error 2 consisted of the interactions of individual animals-within-animal species x sub-plot effects and the relevant individual animals-within-animal species x main plot x sub-plot effects. The residual error term consisted of individual animals-within-animal species x sub-sub-plot effects and the relevant individual animals-within-animal species x main plot x sub-plot x sub-sub-plot interactions. It also contained interactions not taken out by the analysis of variance. In all analyses the effect of variation between individual animals within species was tested against the residual error term. In practice this involved dividing the mean square of error 1 by the residual error mean square and using the degrees of freedom for the two errors to obtain the level of significance from the F tables.

The results are presented as two-way tables of means. Due to the unequal number of values contributing to individual means in most of the results of animal measurements, standard errors of difference are given, rather than standard errors. Differences between means were tested for significance only where F was significant (Snedecor and Cochran, 1980). Where F was significant means were separated using Duncan's Multiple Range Test (Little and Hills, 1972) (1) within swards between animal species and (2) within animal species between swards. Differences between means separated in the former manner are indicated by the level of significance given to the SED. Differences between swards ($P < 0.05$) within animal species are indicated by superscripts in the conventional manner.

The data from the depth of grazing estimations was analysed by the x^2-test, the null hypothesis being that there was no difference between the cattle and sheep in the ratio of observations of grazing above or below 16.5 cm from the sward surface.

Following the preliminary analyses of the animal variables in which the animal's ingestive behaviour responses to particular plant communities were examined, the influence of a range of sward variables on the animal's ingestive behaviour was investigated by means of principal component analysis followed by regression analysis.

Principal component analysis "is an attempt to best describe the shape of a multivariate distribution by considering selected linear combinations of the variables $x_1, \ldots, x_p$, rather than the variables themselves" (Bofinger, 1975). The advantage of the technique is that the derived variables, $x_1, \ldots, x_p$, are mathematically independent of one another and thus can be used in further analyses such as multiple regression analysis, which might otherwise be inappropriate if the original x variables were highly correlated. To obtain the principal components of the original variables a variance-covariance matrix is first produced from which the eigenvalues and eigenvectors for each principal component are calculated, using a technique known as Lagrange Multipliers. The eigenvalue of each principal component when expressed as a percentage of the variation accounted for by the total number of variables gives the proportion of the total variation accounted for by that principal component. The eigenvectors are used to interpret the principal components, specifically to give them meaningful names. These named components can be transferred into new variables by summing the standardised products of the original variables from their means and the corresponding loadings of the eigenvectors for each set of samples (Dudzinski, 1975; Jeffers, 1978).

The principal components were calculated using the GENSTAT program (N.A.G., 1980), as were the regression analyses using the new variables derived from the principal components.

RESULTS

General

The measurements made in 1978, 1979 and 1980 were analysed separately as there were some differences between years in the individual animals used and because the number of individual measurements (particularly those of rate of biting) collected over the three years created run-time problems when put into a single analysis with the computer program used.

Since the structure and botanical composition of the vegetation in each community differed from season to season, and from year to year, each of the measurement periods of the communities was considered to have been made on a distinctly separate sward, and thus comparisons between swards refer to comparisons not only between communities but within communities.

Table E3.4

Sward height (cm), herbage mass (kgDM/ha), total green herbage mass (kgDM/ha) and the proportion of green material in the swards in 1978, 1979 and 1980.

Sward and month of measurement	Sward surface height (cm)	Total herbage mass (kgDM/ha)	Total green mass (kgDM/ha)	Proportion green matter in sward
1978				
Ryegrass May-June	11.0 ± 0.56	2990 ± 210	2780 ± 200	0.93
Nardus June	14.2 ± 0.72	14110 ± 227	4290 ± 220	0.30
Agrostis-Festuca July	15.4 ± 0.68	6640 ± 350	2940 ± 310	0.44
Nardus October	15.7 ± 0.53	14310 ± 700	3510 ± 170	0.25
Agrostis-Festuca October	16.2 ± 0.51	5190 ± 370	2600 ± 210	0.50
1979				
Agrostis-Festuca May	3.5 ± 0.12	3370 ± 210	1700 ± 60	0.28
Nardus May	5.7 ± 0.29	10920 ± 2250	1700 ± 230	0.16
Molinia June	10.4 ± 0.33	1900 ± 190	1110 ± 140	0.58
Ryegrass July	10.1 ± 0.91	2610 ± 180	2350 ± 190	0.90
Molinia August	24.1 ± 0.94	3080 ± 230	2320 ± 130	0.75
Agrostis-Festuca September	6.2 ± 0.21	2620 ± 160	1532 ± 93	0.58
Nardus October	11.8 ± 0.42	9620 ± 1970	3520 ± 580	0.37
1980				
Molinia July	18.2 ± 1.23	2640 ± 170	1880 ± 150	0.71
Molinia September	17.0 ± 0.71	1930 ± 250	1060 ± 110	0.55

Sward conditions: The main characteristics of the swards are described in Table E3.4, the swards being listed in chronological order. Appendix Tables E3.2.1 to E3.2.3 give the weight (kg DM/ha) of the main components in the sward before grazing, and Appendix Tables E3.3.1 to E3.3.3 give the proportions of the same components in the sward. Both the *Nardus* and *Agrostis-Festuca* communities showed quite large reductions in total herbage mass over the two years as a result of the management of the swards between measurement periods.

Appendix Figures E3.1.1 to E3.1.14 show the vertical distribution of the sward components. These figures indicate the horizons in which the bulk of the herbage lay. Appendix Figures E3.1.4, E3.1.5 and E3.1.12 give the impression that the density of the major components was very low at and below 3 cm. This may not have been the case but may rather be a reflection of the difficulty in determining point contacts in the very lowest levels of relatively dense vegetation.

Appendix Tables E3.4.1 to E3.4.14 give the number of hits per 100 points of the major sward components in successive 6 cm horizons. The observations were grouped into 6 cm horizons from the original 3 cm horizons in order to avoid a large number of horizons without any values.

Live weights: The mean live weights of the fistulated and non-fistulated cattle and sheep are given in Table E3.5. Since the numbers of animals in each class did not vary within year except where a whole class was missing, single SED's are given for the comparisons between non-fistulates and fistulates within animal species, for the 1978 and 1979 data. The weights of the animals on the *Molinia* swards in 1980 are given whilst the mean and standard error given is for the mean live weight of the animals over the

Table E3.5

The mean live weights of the non-fistulated (NF) and fistulated (OF) cattle and sheep

Swards and month of measurement	Cattle NF	Cattle OF	Cattle SED	Sheep NF	Sheep OF	Sheep SED
1978						
Ryegrass May - June	431	469		57	52	
Nardus June	493	525		58	47	
Agrostis-Festuca July	530	558	21.5 NS	60	48	3.3 NS
Nardus October	584	624		62	-	
Agrostis-Festuca October	546	581		66	55	
1979						
Agrostis-Festuca May	-	-		60	-	
Nardus May	549	546		62	54	
Molinia June	537	519		63	54	
Ryegrass July	562	560		65	48	
Molinia August	582	575 ±	28.0 NS	66	59 ±	3.8 NS
Agrostis-Festuca September	598	-		-	-	
Nardus October	613	-		66	-	
1980						
Molinia July	599± 22.0	570± 22.7		65± 2.9	48± 1.9	
Molinia September	634± 22.1	-		68± 2.3	-	

whole grazing season and not just the two Molinia swards, since this value was used in the calculation of HOMILW and other calculations involving live weight.

Width of mouth parts: The mean width of the mouths of the cattle and sheep in 1980 was 8.8 ± 0.17 and 3.2 ± 0.06 cm respectively. All the animals had a full complement of incisors, though some of the sheep, particularly two of the oesophageal fistulates, had gaps between the teeth.

Diet digestibility: The mean organic matter digestibilities of the diets obtained by the fistulated cattle and sheep from the range of swards are given in Table E3.6. The coefficients of variation for the three years were respectively 7.3%, 5.1% and 4.1%. Variation between individuals within animal species was not significantly greater than the residual variation in 1978 or 1979 but was in 1980 ($P < 0.01$). Between-day differences were significant only in 1979 ($P < 0.01$) and 1980 ($P < 0.001$), and there were no day x animal species or day x animal species x sward interactions in any year. Of the main effects, swards were significantly different in all three years ($P < 0.001$ in 1978 and 1979; $P < 0.01$ in 1980), but animal species were only significantly different in 1979. The mean values for the cattle and sheep respectively were: 1978 - 0.71 ± 0.009 vs 0.71 ± 0.010; $P > 0.05$: 1979 - 0.70 ± 0.003 vs 0.76 ± 0.003; $P < 0.001$: 1980 - 0.70 ± 0.014 vs 0.72 ± 0.016; $P > 0.05$). The animal species x sward interaction was only significant in 1979 ($P < 0.05$). The full analysis of variance is given in Appendix Table E3.5 Over the three years the sheep obtained diets higher in OMD than the cattle on all but one sward, though the differences were only significant on 5 of the 14 occasions (Table E3.6). Table E3.6 also

Table E3.6

The *in vitro* organic matter digestibility of the diets selected by oesophageal fistulated cattle and sheep

Sward and month of measurement	Organic Matter Digestibility		
	Cattle	Sheep	SED
1978 (+)			
Ryegrass May-June	0.81	0.81	0.026
Nardus June	0.70	0.72	0.028
Agrostis-Festuca July	0.70	0.70	0.026
Nardus October	0.71	0.72	0.026
Agrostis-Festuca October	0.68	0.68	0.027
1979			
Agrostis-Festuca May	(7) 0.63 [e]	(4) 0.75 [b]	0.019***
Nardus May	(3) 0.71 [bc]	(2) 0.79 [a]	0.019***
Molinia June	(2) 0.75 [ab]	(3) 0.77 [a]	0.018 NS
Ryegrass July	(1) 0.78 [a]	(1) 0.80 [a]	0.018 NS
Molinia August	(4) 0.69 [cd]	(6) 0.74 [bc]	0.018*
Agrostis-Festuca September	(5) 0.69 [cd]	(5) 0.74 [bc]	0.018**
Nardus October	(6) 0.67 [d]	(7) 0.72 [c]	0.018*
1980 (+)			
Molinia July	0.74	0.76	0.027
Molinia September	0.66	0.69	0.026

Numbers of values contributing to means ranged from 8 to 11 in 1978, from 10 to +2 in 1979 and from 8 to 11 in 1980.

Numbers in brackets rank the swards in descending order of magnitude separately for the cattle and sheep. Differences between swards within-animal species are indicated by superscrips. Values with different superscripts are significantly different ($P < 0.05$). Differences between animal species are indicated by the SED's.

(+) Sward x animal interaction not significant.

ranks the swards in order of decreasing OMD and indicates the differences in OMD between the swards. It is apparent that cattle and sheep responded differently to the indigenous swards.

<u>Herbage intake</u>: Table E3.7 gives the mean herbage intakes (gOM/kgLW - HOMILW) of the cattle and sheep. Intake was expressed as gOM/kgLW rather than gOM/kgLW$^{0.75}$ as the experiment was primarily concerned with the examination of responses rather than the determination of absolute values, and there is some argument as to what exponent should be used, particularly in comparisons between cattle and sheep (Graham, 1972). Though the coefficient of variation was slightly higher in the 1978 and 1979 analyses when using gOM/kgLW rather than gOM/kgLW$^{0.75}$, it was fractionally lower in the 1980 analysis.

The coefficients of variation for the 1978, 1979 and 1980 analyses were, respectively, 11.4%, 11.5% and 8.0%. Variation between individuals within animal species was significantly greater than the residual variation in all three years ($P < 0.001$ in 1978 and 1979, $P < 0.01$ in 1980). In the overall analysis significant differences were found between swards ($P < 0.01$ in all three years), between animal species (1978: cattle 22.9 ± 1.57 vs sheep 30.8 ± 1.31; $P < 0.01$. 1979: cattle 19.3 ± 1.20 vs sheep 24.6 ± 1.25; $P < 0.01$. 1980: cattle 19.5 ± 1.30 vs sheep 27.9 ± 1.30; $P < 0.001$) and in the sward x animal species interaction ($P < 0.01$ in 1978 and 1980, $P < 0.001$ in 1979). The full analysis of variance is given in Appendix Table E3.6. Table E3.7 also ranks the swards, in the different years, in order of decreasing HOMILW and indicates the differences between the swards.

Table E3.7

Herbage intakes (gOM/kgLW) of the cattle and sheep on all swards in 1978, 1979 and 1980

Sward and month of measurement	Cattle	Sheep	SED
1978			
Ryegrass May - June	(5) 17.9 [c]	(5) 24.5 [d]	2.74**
Nardus June	(2) 25.9 [ab]	(4) 28.0 [c]	2.58 NS
Agrostis-Festuca July	(1) 26.8 [a]	(1) 38.0 [a]	2.58***
Nardus October	(3) 22.2 [b]	(3) 30.7 [bc]	2.58**
Agrostis-Festuca October	(4) 22.0 [b]	(2) 32.8 [b]	2.73**
1979			
Agrostis-Festuca May	(7) 13.7 [c]	(7) 21.1 [d]	2.31**
Nardus May	(3) 21.1 [a]	(2) 26.9 [a]	2.31*
Molinia June	(1) 22.2 [a]	(4) 24.2 [bc]	2.11 NS
Ryegrass July	(2) 21.4 [a]	(3) 24.8 [b]	2.11 NS
Molinia August	(4) 20.5 [a]	(5) 23.1 [c]	2.11 NS
Agrostis-Festuca September	(6) 18.0 [b]	(1) 29.6 [a]	2.11***
Nardus October	(5) 18.2 [b]	(6) 22.5 [cd]	2.11 NS
1980			
Molinia July	(1) 21.4 [a]	(1) 32.9 [a]	2.49 ***
Molinia September	(2) 17.5 [b]	(2) 22.9 [b]	2.49 NS

Numbers of values contributing to means ranged from 5 to 8 in 1978, from 5 to 7 in 1979 and were equal (7) in 1980.

Intakes per bite: Intakes per bite (mgOM/kgLW/bite) were calculated from the HOMILW of the non-fistulated cattle and sheep divided by the total bites per day of the same animals. The mean intakes per bite are given in Table E3.8. The coefficients of variation for the analyses in 1978, 1979 and 1980 were 15.0%, 13.4% and 9.3% respectively. Variation between individuals within animal species was significantly greater than the residual variation in all three years ($P < 0.01$ in 1978 and 1980, $P < 0.001$ in 1979). In the overall analysis differences between swards were significant ($P < 0.001$ in all years) as were differences between animal species (1978: cattle 0.76 ± 0.029 vs sheep 1.09 ± 0.030; $P < 0.01$. 1979: cattle 0.51 ± 0.017 vs sheep 0.87 ± 0.018; $P < 0.001$. 1980: cattle 0.85 ± 0.031 vs sheep 1.18 ± 0.029; $P < 0.01$). The sward x animal interaction was only significant in 1979 and 1980 ($P < 0.001$). The complete analysis of variance is given in Appendix Table E3.7. Table E3.8 ranks the swards in 1979 and 1980 in decreasing order of intake per bite and indicates the differences between the swards.

Weights per bite per kgLW were also estimated in 1978 and 1979 by recording the number of bites taken during the collection of extrusa samples before converting the data to give mgOM/kgLW. Attempts were made to collect 100% of the material ingested by the use of foam-rubber plugs inserted into the oesophagus below the fistula. In 1978 this proved singularly unsuccessful with the sheep and weights per bite were not obtained by this method except on the ryegrass sward. The method was not used in 1980, nor was it used with the sheep in 1979 on the August Molinia sward, as the height of the sward prevented accurate counting of the number of bites taken by the sheep over the whole collection period. Variation

Table E3.8

Mean intakes per bite (mgOM/kgLW) for cattle and sheep in 1978, 1979 and 1980. Values are calculated from mean daily intakes (gOM/kgLW) of non-fistulated animals divided by total bites per day.

Sward and month of measurement	Cattle	Sheep	SED
1978 (†)			
Ryegrass May - June	0.56	0.94	0.129
Nardus June	0.98	1.14	0.115
Agrostis-Festuca July	0.95	1.36	0.129
Nardus October	0.70	1.07	0.122
Agrostis-Festuca October	0.62	0.93	0.122
1979			
Agrostis-Festuca May	(7) 0.29[c]	(7) 0.44[d]	0.087 NS
Nardus May	(5) 0.49[ab]	(3) 0.84[b]	0.087***
Molinia June	(3) 0.58[ab]	(1) 1.29[a]	0.081***
Ryegrass July	(2) 0.60[ab]	(4) 0.78[b]	0.081*
Molinia August	(1) 0.61[a]	(2) 1.20[a]	0.081***
Agrostis-Festuca September	(6) 0.45[b]	(5) 0.72[bc]	0.087*
Nardus October	(4) 0.52[ab]	(6) 0.58[cd]	0.087 NS
1980			
Molinia July	(1) 0.98[a]	(1) 1.63[a]	0.114***
Molinia September	(2) 0.72[b]	(2) 0.73[b]	0.119 NS

The number of values contributing to the means varied between 4 and 5 in 1978, 3 and 4 in 1979 and 5 and 6 in 1980.

(†) Sward x animal interaction not significant.

Table E3.9

Mean weights per bite (mg OM/kg LW) for cattle and sheep in 1979. Values are calculated from the number of bites taken during collection of known weights of extrusa.

Sward and month of measurement		Cattle		Sheep	SED
Agrostis-Festuca May	(7)	0.35^{c}	(6)	0.57^{c}	0.214 NS
Nardus May	(5)	0.51^{c}	(4)	0.90^{bc}	0.221 NS
Molinia June	(2)	1.45^{ab}	(1)	1.72^{a}	0.231 NS
Ryegrass July	(1)	1.67^{a}	(2)	1.05^{b}	0.225^{*}
Molinia August	(3)	1.11^{b}		-	-
Agrostis-Festuca September	(6)	0.36^{c}	(3)	0.96^{b}	0.210*
Nardus October	(4)	0.55^{c}	(5)	0.72^{bc}	0.295 NS
Mean and Standard Error		0.84 ±0.059		1.00 ±0.06	

The number of values contributing to the means ranged from 4 to 12.

between individuals within-animal species was not significantly greater than the residual variation, neither were there any differences between days. In the overall analysis animal species were not significantly different but swards were ($P < 0.001$); the sward x animal species interaction was also significant ($P < 0.001$). The complete analysis of variance is given in Appendix Table E3.8. Table E3.9 gives the mean weights per bite on the different swards and shows the swards ranked in decreasing order. Cattle and sheep responded differently to the swards with the largest weights per bite by the cows being on the ryegrass and Molinia swards. The sheep did not show a clear-cut response.

A comparison of the two techniques indicated that there was a significant ($P < 0.01$) difference overall between them, with intakes per bite calculated from HOMILW and total daily bites being 27% lower than those derived from the weight of extrusa collected (0.67 vs 0.92 mgOM/kgLW.SED = 0.026). The technique x animal species and technique x animal species x sward interactions were not significant. Table E3.10 gives the intakes per bite of the cattle and sheep measured by the two techniques on each sward. Since the same number of cattle were used for both techniques only one SED is given for within-sward between-treatment comparisons in the cattle, while individual SED's are given for between-treatment comparisons in the sheep. Levels of significance are not however given since the F ratio for the treatment x animal species x sward interaction was not significant (Appendix Table E3.9). The major differences between the techniques appeared to occur on the Molinia and ryegrass swards in both cattle and sheep with differences on the Agrostis-Festuca and Nardus swards being relatively minor.

Table E3.10

Intakes per bite (mg OM/kg LW) calculated from HOMILW and total daily bites (T1), and from the number of bites taken during collection of extrusa samples (T2) during 1979.

Swards	Cattle			Sheep		
	T1	T2	SED	T1	T2	SED
Agrostis-Festuca May	0.29	0.34		0.44	0.58	0.235NS
Nardus May	0.49	0.50		0.84	0.90	0.235NS
Molinia June	0.58	1.47		1.29	1.69	0.218NS
Ryegrass July	0.60	1.69	0.218+NS	0.78	1.03	0.218NS
Molinia August	0.61	1.03		1.20	-	-
Agrostis-Festuca September	0.45	0.36		0.72	0.96	0.235NS
Nardus October	0.52	0.54		0.58	0.72	0.235NS

+ All cattle values are means of 4 animals so a single SED is applicable. For sheep the number of values contributing to the means ranged from 2 to 4.

<u>Rates of biting</u>: The analyses of variance indicated that there were no significant differences between fistulated and non-fistulated cattle and sheep in biting rate, so the values presented in Table E3.11 are the overall means of pairs of observations made on all the cattle and sheep over four days of the measurement week in 1978 and 1979 and over two days in 1980. Coefficients of variation for the three analyses were 11.4%, 9.4% and 13.6%. Variation between individual animals within-animal species was significantly greater than the residual variation ($P < 0.001$ in 1978 and 1979, $P < 0.01$ in 1980). Between-day differences within years were only significant in 1980 ($P < 0.001$) when the intensity of observation was very much greater. The overall analysis revealed that the sward effects were significant in all years ($P < 0.001$) as was the animal species effect (1978: cattle 54 ± 1.18 vs sheep 50 ± 1.07; $P < 0.05$. 1979: cattle 61 ± 0.90 vs sheep 57 ± 0.85; $P < 0.001$. 1980: cattle 45 ± 0.78 vs sheep 47 ± 0.67; $P < 0.05$). The sward x animal species interaction was significant in all years ($P < 0.05$ in 1979 and 1980, $P < 0.001$ in 1979). The full ANOVA results are given in Appendix Table E3.10. Cattle had faster rates of biting than the sheep on all the swards measured in 1978 and 1979, though they had slower rates of biting on the two <u>Molinia</u> swards measured in 1980. However only seven of the fourteen differences were significant at the 5% level. Table E3.11 also shows the swards in the different years ranked in order of decreasing rate of biting and indicates the differences between the swards.

Rates of biting did not change consistently between days as grazing progressed in either the cattle or the sheep.

The effect of season on rate of biting in 1978 and 1979 was

Table E3.11

The mean rates of biting (bites/min) by the cattle and sheep

Sward and month of measurement	Cattle	Sheep	SED
1978			
Ryegrass May - June	(3) 55 [bc]	(3) 53[b]	±2.22NS
Nardus June	(5) 47 [d]	(5) 39[c]	±2.15*
Agrostis-Festuca July	(2) 56 [ab]	(1) 57[a]	±2.24NS
Nardus September	(4) 53 [c]	(4) 48[d]	±1.92*
Agrostis-Festuca October	(1) 59 [a]	(2) 55[ab]	±2.06NS
1979			
Agrostis-Festuca May	(1) 73 [a]	(1) 71[a]	±2.05NS
Nardus May	(3) 65 [b]	(4) 57[c]	±1.72***
Molinia June	(6) 53 [d]	(6) 44[d]	±1.97***
Ryegrass July	(5) 59 [c]	(3) 58[bc]	±1.85NS
Molinia August	(7) 50 [e]	(7) 43[d]	±1.71***
Agrostis-Festuca September	(2) 70 [a]	(2) 70[a]	±1.72 NS
Nardus October	(4) 61 [c]	(5) 56[c]	±1.98 **
1980			
Molinia July	(2) 44 [a]	(2) 44[b]	±1.25 NS
Molinia September	(1) 45 [a]	(1) 50[a]	±1.48 **

The number of values contributing to the means ranged from 26 to 46 in 1978, from 30 to 51 in 1979 and from 81 to 150 in 1980.

Table E3.12

The significance of animal, day, period-within-day effects and animal x period within-day interactions for the five swards measured in 1980

Swards	A	D	P	PxA
Agrostis-Festuca (July)	*	**	***	NS
Molinia (July)	NS	***	*	*
Nardus (July)	NS	***	***	*
Agrostis-Festuca (August)	NS	NS	***	NS
Molinia (September)	**	***	***	NS

A = animal species

D = days

P = periods-within-days

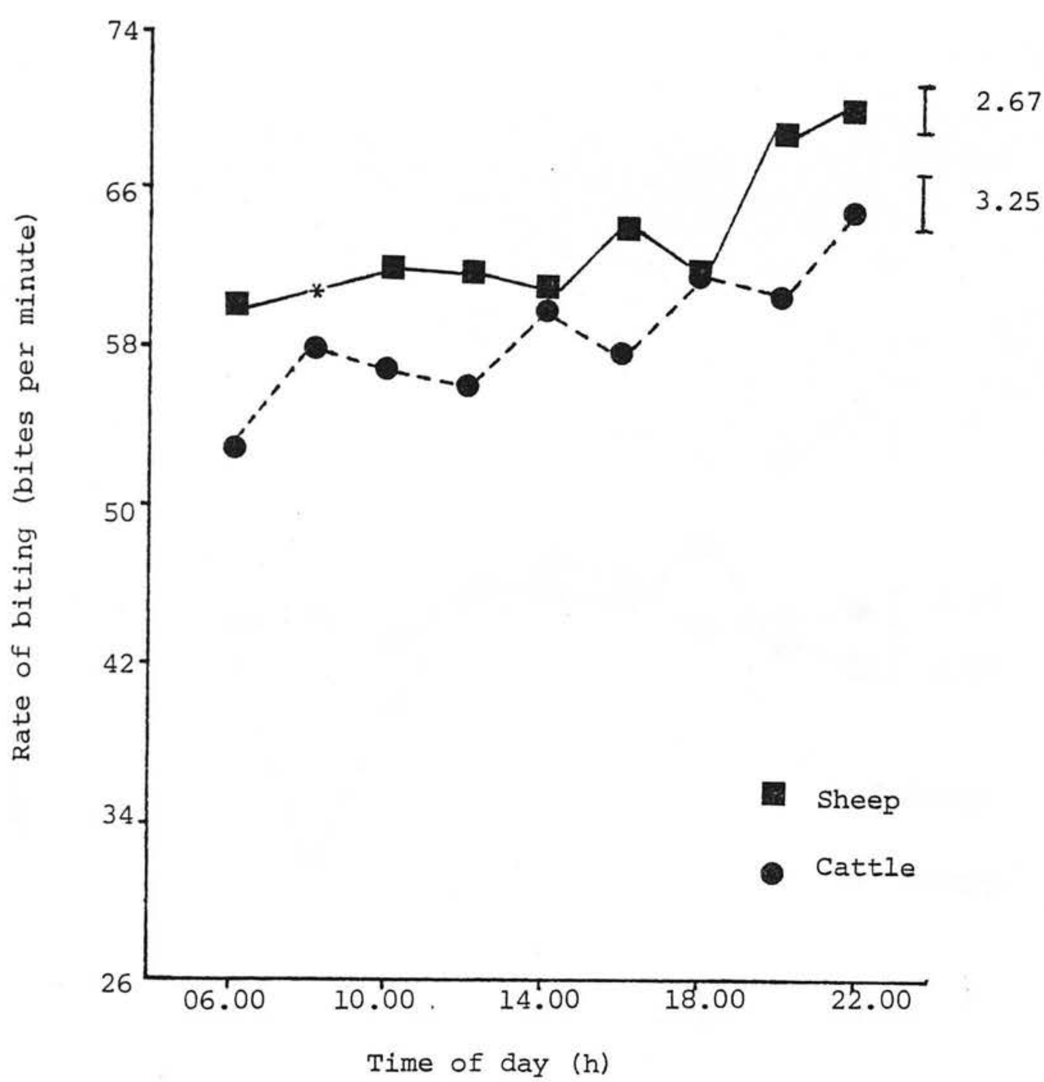
PxA = Period-within-day x animal species interaction examined and found to be significant ($P < 0.001$) in both years, with rates of biting being faster in the autumn of 1978 but slower in the autumn of 1979 relative to measurements made early in each year.

Insufficient records were collected in 1978 and 1979 to allow examination of diurnal changes in rate of biting so in 1980 intensive measurements were made on the Agrostis-Festuca sward in July and August, on the Molinia sward in July and September and on the Nardus sward in July. Rates of biting were recorded on all animals over two days in successive two-hour periods beginning at dawn and ending at dusk (04.00h to 22.00h in July and 06.00h to 20.00h in September). Due to the size of the data files analyses had to be carried out separately for each sward. Table E3.12 summarises the analyses of variance carried out. Day x animal interactions were only significant on the Agrostis-Festuca and Molinia swards in July. The full results are given in Appendix Tables E3.11.1 to E3.11.5. Figures E3.2 to E3.6 show the diurnal changes in rate of biting by the cattle and sheep on the five swards.

Grazing time: The mean grazing times (mins/day) of the non-fistulated cattle and sheep are presented in Table E3.13. Each value is the mean of the total number of complete 24h records collected from the cattle and sheep over the 4-day measurement period. The mean values have been rounded to the nearest five minutes. Coefficients of variation for the three analyses were for 1978, 1979 and 1980 respectively 11.1%, 9.6% and 8.1%. Between-individual-animal variation was significantly greater than the residual variation in all years ($P < 0.001$ for each year) whilst between-day within-year differences were only significant in 1980

Figure E3.2

Cattle and sheep rates of biting at two-hour intervals on the July, 1980 Agrostis-Festuca sward. (Each value is the mean of between 2 and 10 observations on each of 11 cows and 13 sheep over two days).

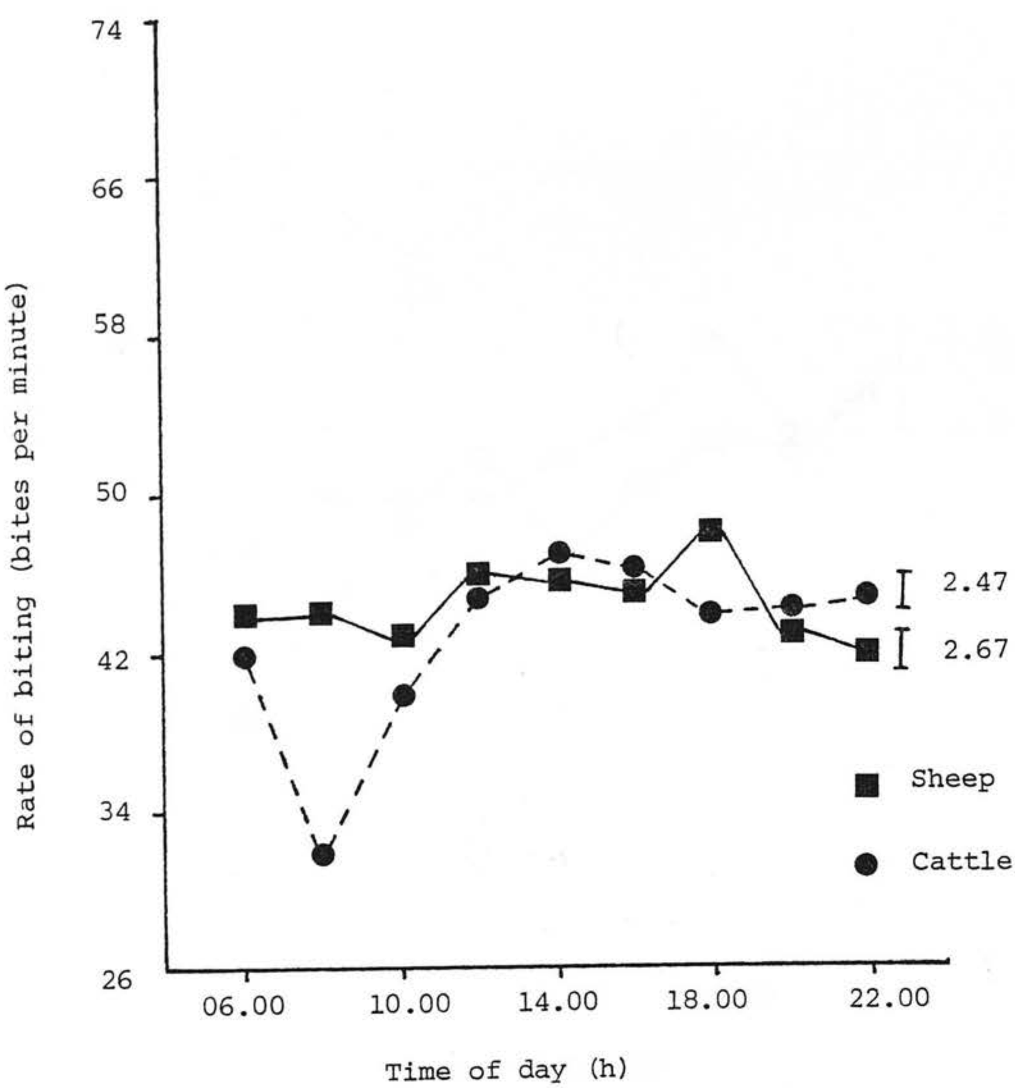


* = No animals grazing

I = Confidence limits (95%)

Figure E3.3

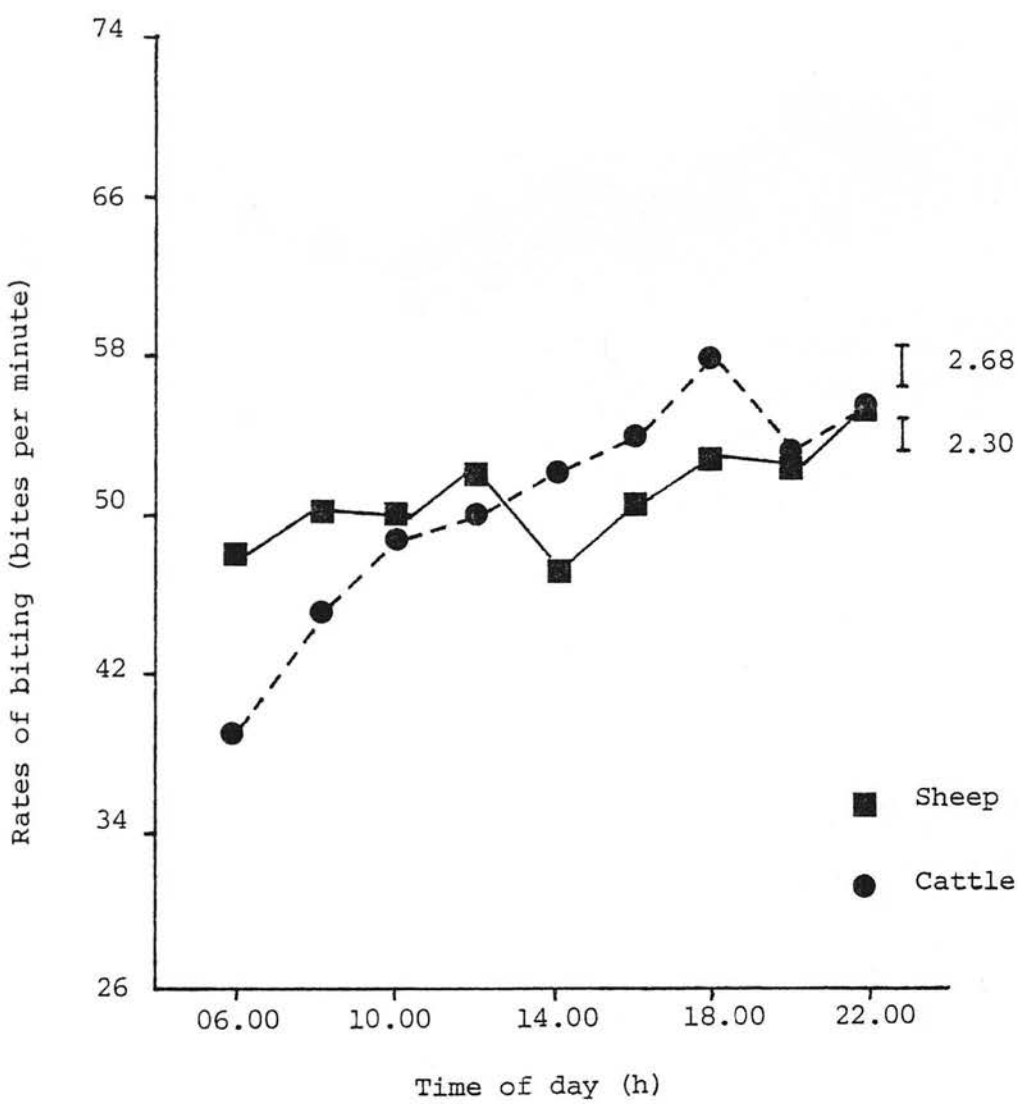
Cattle and sheep rates of biting at two-hour intervals on the July 1980 Molinia sward. (Each value is the mean of between 2 and 10 observations on each of 11 cows and 13 sheep over two days).



I = Confidence limits (95%)

Figure E3.4

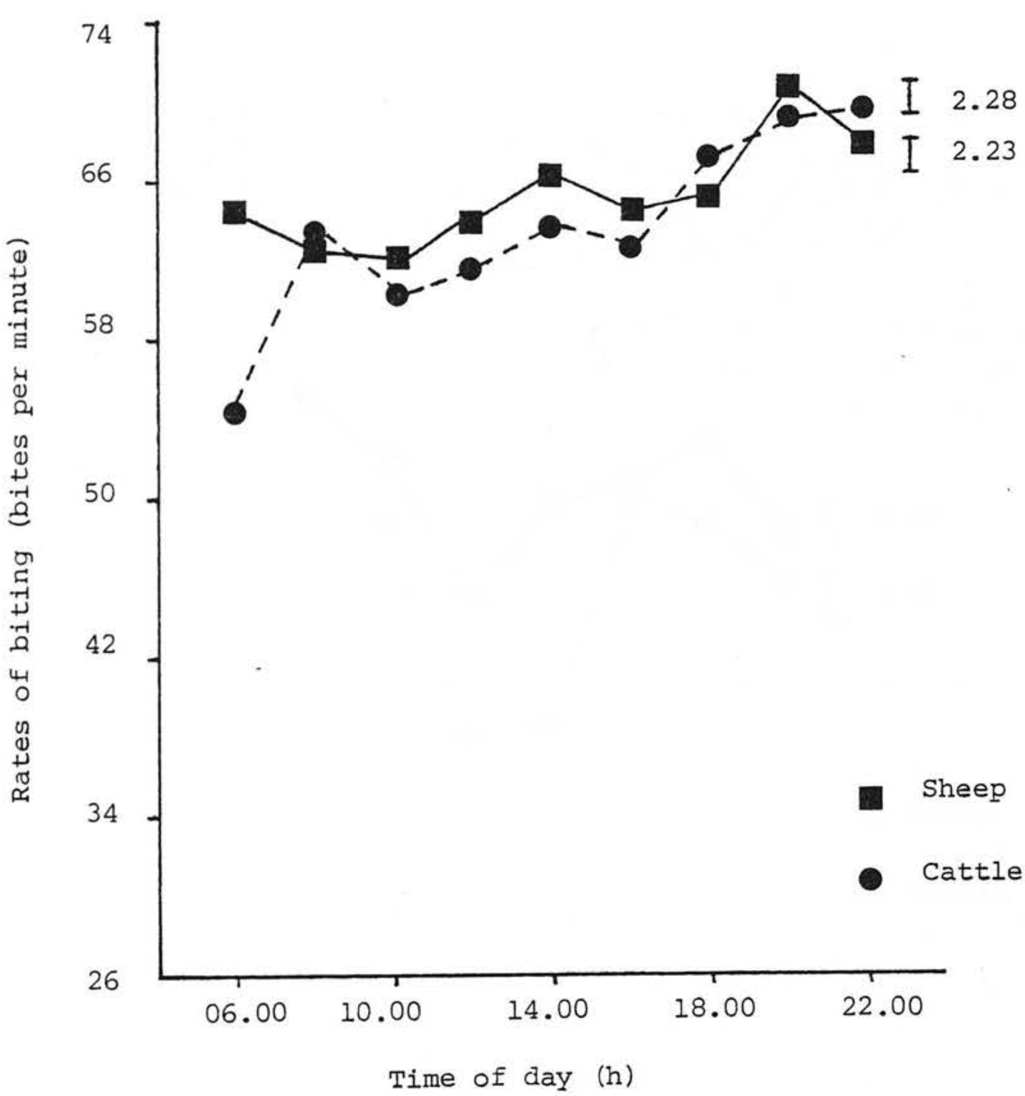
Cattle and sheep rates of biting at two-hour intervals on the July 1980 Nardus sward. (Each value is the mean of between 2 and 10 observations on each of 11 cows and 12 sheep over two days).



I = Confidence limits (95%)

Figure E3.5

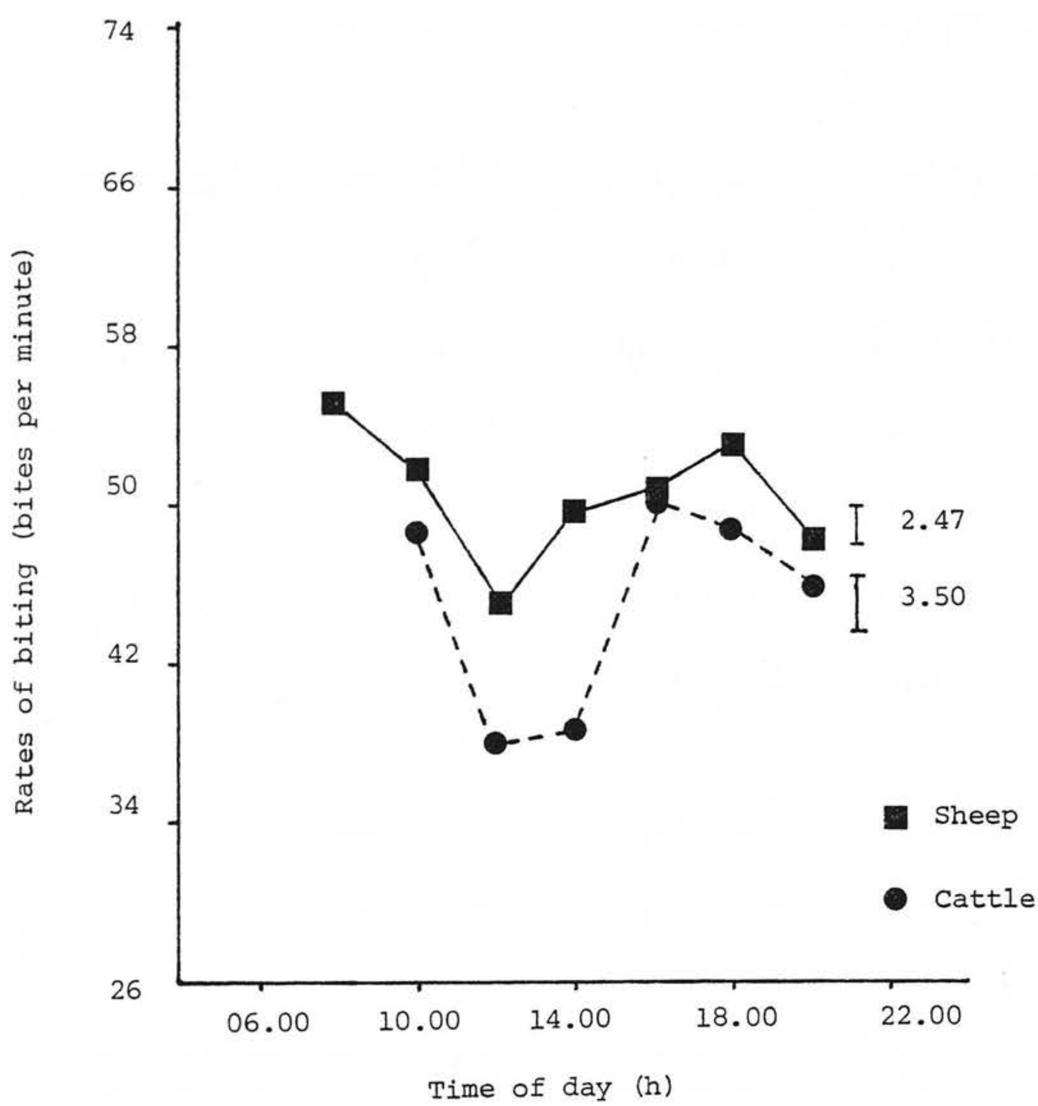
Cattle and sheep rates of biting at two-hour intervals on the August 1980 Agrostis-Festuca sward. (Each value is the mean of between 2 and 10 observations on each of 11 cows and 12 sheep over two days)



I = Confidence limits (95%)

Figure E3.6

Cattle and sheep rates of biting at two-hour intervals on the September 1980 Molinia sward. (Each value is the mean of between 2 and 10 observations on each of 11 cows and 12 sheep over two days.



I = Confidence limits (95%)

Table E3.13

The mean time (mins) spent grazing by the non-fistulated cattle and sheep

Sward and month of measurement	Cattle	Sheep	SED
1978			
Ryegrass May - June	(3) 570 [a]	(4) 510 [b]	29.9 NS
Nardus June	(1) 575 [a]	(3) 600 [a]	26.7 NS
Agrostis-Festuca July	(5) 485 [b]	(5) 485 [b]	33.3 NS
Nardus September	(2) 575 [a]	(2) 610 [a]	29.5 NS
Agrostis-Festuca October	(4) 560 [a]	(1) 610 [a]	31.1 NS
1979			
Agrostis-Festuca May	(4) 625 [bc]	(1) 685 [a]	35.3 NS
Nardus May	(3) 660 [ab]	(3) 620 [a]	32.1 NS
Molinia June	(1) 695 [a]	(7) 460 [c]	33.1 ***
Ryegrass July	(5) 595 [cd]	(5) 535 [b]	32.6 NS
Molinia August	(2) 665 [a]	(6) 500 [bc]	31.0***
Agrostis-Festuca September	(7) 560 [d]	(4) 615 [a]	35.1 NS
Nardus October	(6) 570 [d]	(2) 650 [a]	34.5 *
1980			
Molinia July	(2) 485 [a]	(2) 455 [b]	29.1 NS
Molinia September	(1) 500 [a]	(1) 600 [a]	28.7 **

The number of values contributing to the means ranged from 13 to 20 in 1978, from 11 to 16 in 1979 and from 19 to 20 in 1980.

($P < 0.01$). Sward effects were significant in all years ($P < 0.001$ in 1978, $P < 0.01$ in 1979 and 1980) whilst the animal species effect was significant only in 1979, (1978: cattle 555 ± 14.9 vs sheep 565 ± 14.9; $P > 0.05$. 1979: cattle 625 ± 10.7 vs sheep 580 ± 10.9; $P < 0.001$. 1980: cattle 495 ± 16.7 vs. sheep 530 ± 16.4; $P > 0.05$). The sward x animal interaction was significant in all three years ($P < 0.05$ in 1978, $P < 0.001$ in 1979, $P < 0.01$ in 1980). The full ANOVA results for the three years are given in Appendix Table E3.12. Cattle and sheep responded differently to the swards as indicated by Table E3.13, as a result of which neither species had consistently longer or shorter grazing times over all the swards.

The effect of season on grazing time in 1978 and 1979 was examined and found to be significant ($P < 0.001$ in 1978; $P < 0.05$ in 1979). Grazing times were longer in the autumn than the spring of 1978 in both the cattle and the sheep. In 1979 the effect was not so clear. The cattle grazed for longer in the early measurement periods than they did in the later periods irrespective of sward type whilst the sheep only grazed longer early in the year on the Agrostis-Festuca sward.

Diet composition: The proportions of the major components in the diets of the cattle and sheep as determined by the separation of extrusa samples are given in Tables E3.14.1 to E3.14.7. The number of values contributing to each mean was the same for each component within each year, ranging from 10 to 15 in 1978 and 1980 and from 9 to 12 in 1979. Table E3.15 shows the components and years in which the between individual animal variation within animal species was greater than the residual variation.

Table E3.14.1

The proportion of green material (total green) in the diets of the cattle and sheep.

Swards and month of measurement	Cattle	Sheep	SED
1978			
Ryegrass May - June	(1) 0.96[a]	(1) 0.98[a]	0.018 NS
Nardus June	(2=) 0.86[b]	(3) 0.90[b]	0.018 NS
Agrostis-Festuca July	(2=) 0.86[b]	(2) 0.92[b]	0.017 **
Nardus October	(4) 0.72[c]	(4) 0.82[c]	0.018 ***
Agrostis-Festuca October	(5) 0.66[d]	(5) 0.80[c]	0.018 ***
1979			
Agrostis-Festuca May	(7) 0.45[c]	(7) 0.79[d]	0.025 ***
Nardus May	(6) 0.68[b]	(4) 0.89[bc]	0.026 ***
Molinia June	(2) 0.96[a]	(2) 0.97[a]	0.025 NS
Ryegrass July	(1) 0.97[a]	(1) 0.97[a]	0.024 NS
Molinia August	(3) 0.95[a]	(3) 0.92[ab]	0.024 NS
Agrostis-Festuca September	(5) 0.71[b]	(5) 0.85[c]	0.024 ***
Nardus October	(4) 0.72[b]	(6) 0.84[c]	0.026 ***
1980(†)			
Molinia July	0.96	0.95	0.059
Molinia September	0.79	0.69	0.053

(†) Sward x Animal interaction not significant

Table E3.14.2

The proportion of green grass leaf in the diets of the cattle and sheep.

Sward and month of measurement	Cattle	Sheep	SED
1978			
Ryegrass May - June	(1) 0.69[a]	(2) 0.73[a]	0.052 NS
Nardus June	(5) 0.35[c]	(3) 0.61[†b]	0.052***
Agrostis-Festuca July	(3) 0.54[b]	(5) 0.38[†d]	0.049***
Nardus October	(2) 0.56[b]	(1) 0.74[†a]	0.053 **
Agrostis-Festuca October	(4) 0.53[b]	(4) 0.48[†c]	0.053 NS
1979 (††)			
Agrostis-Festuca May	0.41	0.65[†]	0.063
Nardus May	0.57	0.74[†]	0.064
Molinia June	0.52	0.70[†]	0.063
Ryegrass July	0.53	0.58	0.061
Molinia August	0.49[†]	0.65	0.061
Agrostis-Festuca September	0.63	0.75	0.060
Nardus October	0.68[†]	0.79	0.065
1980			
Molinia July	(1) 0.48[a]	(2) 0.47[a]	0.057 NS
Molinia September	(2) 0.17[b]	(1) 0.49[†a]	0.052 ***

† includes chewed grass leaf that could not be identified as broad or fine.

(††) Sward x Animal interaction not significant.

Table E3.14.3

The proportion of broad-leaved grass leaf in the diets of the cattle and sheep.

Swards and month of measurement	Cattle	Sheep	SED
1978			
Ryegrass May	(1) 0.69^{a}	(1) 0.73^{a}	0.046 NS
Nardus June	(5) 0.06^{c}	(4) 0.21^{bc}	0.046 ***
Agrostis-Festuca July	(3) 0.37^{b}	(3) 0.25^{b}	0.043 **
Nardus October	(4) 0.15^{c}	(5) 0.15^{c}	0.047 NS
Agrostis-Festuca October	(3) 0.34^{b}	(2) 0.27^{b}	0.047 NS
1979 (†)			
Agrostis-Festuca May	0.22	0.29	0.074
Nardus May	0.04	0.13	0.076
Molinia June	0.50	0.66	0.074
Ryegrass July	0.53	0.58	0.073
Molinia August	0.46	0.53	0.073
Agrostis-Festuca September	0.36	0.54	0.071
Nardus October	0.20	0.14	0.077
1980			
Molinia July	(1) 0.47^{a}	(1) 0.45^{a}	0.071 NS
Molinia September	(2) 0.16^{b}	(2) 0.28^{b}	0.064 NS

(†) Sward x Animal interaction not significant.

Table E3.14.4

The proportion of fine-leaved grass leaf in the diets of the cattle and sheep.

Swards and month of measurement	Cattle	Sheep	SED
1978			
Ryegrass May - June	-	-	-
Nardus June	(2) 0.29[b]	(2) 0.37[b]	0.058 NS
Agrostis-Festuca July	(4) 0.17[c]	(4) 0.11[c]	0.049 NS
Nardus October	(1) 0.41[a]	(1) 0.57[a]	0.055*
Agrostis-Festuca October	(3) 0.19[bc]	(3) 0.19[c]	0.055 NS
1979			
Agrostis-Festuca May	(4) 0.19[b]	(3) 0.35[b]	0.045**
Nardus May	(1) 0.48[a]	(1) 0.52[a]	0.046 NS
Molinia June	(6) 0.01[c]	(6) 0.01[d]	0.045 NS
Ryegrass July	-	-	
Molinia August	(5) 0.02[c]	(5) 0.06[d]	0.044 NS
Agrostis-Festuca September	(3) 0.27[b]	(4) 0.21[c]	0.043 NS
Nardus October	(2) 0.42[a]	(2) 0.43[ab]	0.046 NS
1980			
Molinia July	(1=) 0.01[a]	(2) 0.01[a]	0.032 NS
Molinia September	(1=) 0.01[a]	(1) 0.20[b]	0.031 ***

Table E3.14.5

The proportion of grass stem[†] and flower in the diets of the cattle and sheep.

Swards and month of measurement	Cattle	Sheep	SED
1978			
Ryegrass May - June	(2) 0.27^{b}	(1) 0.13^{a}	0.029***
Nardus June	(1) 0.44^{a}	(3) 0.11^{ab}	0.029***
Agrostis-Festuca July	(3) 0.22^{b}	(3) 0.07^{bc}	0.027***
Nardus October	(5) 0.08^{c}	(4) 0.05^{c}	0.029 NS
Agrostis-Festuca October	(4) 0.09^{c}	(5) 0.04^{c}	0.029 NS
1979			
Agrostis-Festuca May	(6=) 0.03^{c}	(4) 0.05^{bc}	0.035 NS
Nardus May	(4) 0.07^{c}	(3=) 0.10^{b}	0.035 NS
Molinia June	(3) 0.28^{b}	(1) 0.21^{a}	0.035 *
Ryegrass July	(1) 0.37^{a}	(2) 0.20^{a}	0.024***
Molinia August	(2) 0.32^{ab}	(3=) 0.10^{b}	0.034***
Agrostis-Festuca September	(6=) 0.03^{c}	(6) 0.01^{c}	0.032 NS
Nardus October	(5) 0.04^{c}	(5) 0.02^{c}	0.036 NS
1980 (††)			
Molinia July	0.29	0.15	0.051
Molinia September	0.05	0.04	0.046

† Includes vegetative and flower stem

(††) Sward x Animal interaction not significant.

Table E3.14.6

The proportions of dicots in the diets of the cattle and sheep

Swards and month of measurement	Cattle	Sheep	SED
1978			
Ryegrass May - June	(5) 0.01[a]	(4) 0.13[c]	0.057 NS
Nardus June	(2) 0.07[a]	(3) 0.14[c]	0.057 NS
Agrostis-Festuca July	(1) 0.09[a]	(1) 0.47[a]	0.055 ***
Nardus October	(3) 0.05[a]	(5) 0.03[d]	0.059 NS
Agrostis-Festuca October	(4) 0.03[a]	(2) 0.27[b]	0.059 **
1979			
Agrostis-Festuca May	(2=) 0.01[a]	(3) 0.07[b]	0.039 NS
Nardus May	(5=) + [a]	(6=) 0.01[b]	0.036 NS
Molinia June	(2=) 0.01[a]	(5) 0.03[b]	0.039 NS
Ryegrass July	(1) 0.07[a]	(2) 0.18[a]	0.034 **
Molinia August	(5=) + [a]	(1) 0.19[a]	0.038 ***
Agrostis-Festuca September	(2=) 0.01[a]	(4) 0.04[b]	0.037 NS
Nardus October	(5=) + [a]	(6=) 0.01[b]	0.040 NS
1980 (†)			
Molinia July	+	0.24	0.076
Molinia September	+	0.12	0.069

(†) Sward x Animal interaction not significant.

+ = Trace

Table E3.14.7

The proportion of *Juncus* in the diets of the cattle and sheep on the *Molinia* swards.

Month of measurement	Cattle	Sheep	SED
1979 (†)			
June	(2) 0.12	(1) 0.02	0.049
August	(1) 0.13	(2) +	
1980			
July	(2) 0.16[b]	(1) 0.07[a]	0.069 NS
September	(1) 0.56[a]	(2) 0.01[a]	0.063 ***

(†) Sward x Animal interaction not significant

+ = Trace

Table E3.15

The dietary components and the years where the variation between individual-animals within-animal species was greater than the residual variation.

Dietary components	1978	1979	1980
Total green	NS	NS	***
Total grass leaf	*	**	NS
Broad-leaved grass leaf	NS	**	NS
Fine-leaved grass leaf	***	NS	NS
Total grass stem + flower	**	*	NS
Dicots	***	***	*
Juncus	-	NS	NS

The animal species x sward interaction was significant for all components in 1978, for all components except total grass leaf and broad-leaved grass in 1979 and for all components except total green, total grass stem and flower and dicots in 1980. Overall differences between swards were significant for all components in 1978 and 1979, and for all components except dicots in 1980. The effect of animal species varied between components and years. In 1978 the effect of animal species was only significant for total green, total stem and flower and dicots. In 1979 the animal species effect was significant for all components except broad- and fine-leaved grass whilst in 1980 the effect of animal species was significant for all components except total green and broad-leaved grass. The full analysis of variance results for each component in each year are given in Appendix Tables E3.13 to E3.15.

Depth of grazing: Table E3.16 gives the number of observations per sward where the heads of the cattle and sheep were inserted less than or more than 16.5 cm from the surface into the sward. Of the 14 swards three were too short for the animals to graze deeper than 16.5 cm whilst on the May 1979 Nardus sward all grazing was less than 16.5 cm deep. Of the remaining swards the sheep grazed deeper

Table E3.16

Numbers of observations where the heads of the cattle and sheep were inserted less than or more than 16.5 cm into the sward with the χ^2 value and the height of the sward determined from the highest 'first hits' of the point quadrat measurements

Sward and Month		Number of Observations <16.5 cm	>16.5 cm	χ^2	Sward Height (cm)
1978					
Ryegrass	Cattle	64	0	-	17.0
May - June	Sheep	76	0		
Nardus	Cattle	109	13	63.0***	25.5
June	Sheep	56	78		
Agrostis-Festuca	Cattle	74	36	36.9***	34.0
July	Sheep	33	82		
Nardus	Cattle	126	93	1.8 NS	25.5
October	Sheep	133	126		
Agrostis-Festuca	Cattle	129	24	18.2***	34.5
October	Sheep	137	2		
1979					
Agrostis-Festuca	Cattle	84	0	-	11.0
	Sheep	130	0		
Nardus	Cattle	110	0	-	23.0
May	Sheep	173	0		
Molinia	Cattle	70	18	34.9***	23.0
June	Sheep	34	60		
Ryegrass	Cattle	78	0	26.3***	25.5
July	Sheep	125	47		
Molinia	Cattle	11	133	1.07 NS	54.0
August	Sheep	11	209		
Agrostis-Festuca	Cattle	110	0	-	17.0
September	Sheep	200	0		
Nardus	Cattle	96	7	22.5***	23.0
October	Sheep	78	38		
1980					
Molinia	Cattle	106	119	11.4***	42.0
July	Sheep	80	170		
Molinia	Cattle	41	100	9.0 **	39.0
September	Sheep	97	119		

than the cattle on all swards except the October 1978 Agrostis-Festuca and the September 1980 Molinia swards.

The sward heights used differ from those given in Table E3.4 in that they represent the tallest components of the swards, rather than the mean heights of the sward.

Selection ratios: The calculated selection ratios are given in Tables E3.17.1 to E3.17.3. Both cattle and sheep showed apparent selection for total green and, apart from the cattle on the September 1980 Molinia sward, for grass leaf. Cattle selected for total stem in those periods when grass flower stems were at an early immature stage, and avoided total stem in the early spring and autumn periods. Sheep showed a selection for total stem only on the May 1979 Nardus sward, where the stem component was mainly vegetative stem (Appendix Table E3.17), otherwise they appeared to avoid stem. Sheep, apart from in September 1979 on the Agrostis-Festuca sward, consistently had high selection ratios for dicots. Cattle only showed selection for dicots on 4 of the 14 swards.

Since components that have high proportions in the sward cannot give high selection ratios the actual size of the ratios may be misleading.

The length of herbage removed during grazing: The means and standard errors of the pre- and post-grazing measurements on the extended length of grass leaves are given in Table E3.18. No results are given for flower stems as few were 'hit' during pregrazing measurements and few were grazed. The animals did not always graze the transects and for completeness extended leaf measurements were made on 50 ungrazed leaves adjoining grazed areas on which between 100 and 200 extended leaf measurements were made.

Table E3.17.1

Selection ratios calculated from proportions of components in cattle and sheep diets and proportions of components in the swards in 1978

Components	Ryegrass May-June		Nardus June		Agrostis-Festuca July		Nardus October		Agrostis-Festuca October	
	Cows	Sheep	Cows	Sheep	Cows	Sheep	Cows	Sheep	Cows	Sheep
Total green	1.04	1.05	2.83	2.95	1.95	2.08	2.90	3.25	1.31	1.59
Total grass leaf	1.17	1.24	2.78	4.78	2.61	1.87	4.57	5.42	2.28	1.96
Broad-leaved grass	1.17	1.24	8.55	28.03	8.73	6.01	21.23	18.49	3.67	2.75
Fine-leaved grass	-	-	2.41	3.07	1.04	0.64	3.54	4.46	1.37	1.35
Grass stem and flower	0.94	0.45	3.57	0.91	1.37	0.40	0.76	0.52	0.53	0.26
Dicots	0.19	3.50	1.46	3.66	1.41	7.66	1.66	2.97	0.40	3.40
Dead	0.49	0.29	0.20	0.15	0.25	0.14	0.38	0.27	0.69	0.41

Table E3.17.2

Selection ratios calculated from proportions of components in cattle and sheep diets and proportions of components in the swards in 1979

Components	Agrostis-Festuca May		Nardus May		Molinia June		Ryegrass July		Molinia August		Agrostis-Festuca September		Nardus October	
	Cows	Sheep	Cows	Sheep	Cows	Sheep	Cows	Sheep	Cows	Sheep	Cows	Sheep	Cows	Sheep
Total green	1.63	2.83	4.39	5.68	1.65	1.66	1.06	1.08	1.26	1.22	1.46	1.73	1.97	2.30
Total grass leaf	3.18	5.07	7.68	10.28	1.48	1.99	1.08	1.19	1.13	1.52	2.81	3.32	3.43	4.00
Broad-leaved grass	4.71	6.47	50.59	78.82	1.88	2.46	1.08	1.19	1.23	1.40	4.49	6.66	7.31	5.28
Fine-leaved grass	2.33	4.21	6.69	7.13	0.17	0.09	-	-	0.33	1.15	1.86	1.44	2.76	2.52
Grass stem and flower	0.26	0.43	0.94	1.26	1.37	0.99	0.95	0.54	1.33	0.31	0.18	0.08	0.23	0.13
Dicots	0.57	4.86	0.57	2.08	0.75	2.62	4.11	12.80	0.29	7.46	0.12	0.46	0.25	1.07
Juncus	-	-	-	-	-	-	-	-	35.83	1.11	-	-	-	-
Dead	0.76	0.30	0.65	0.25	0.07	0.08	0.40	0.28	0.22	0.32	0.56	0.30	0.44	0.25

Table E3.17.3

Selection ratios calculated from proportions of components in cattle and sheep diets and proportions of components in the swards in 1980

Sward	Molinia July		Molinia September	
Component	Cattle	Sheep	Cattle	Sheep
Total green	1.36	1.34	1.45	1.27
Total grass leaf	1.08	1.05	0.53	1.49
Broad-leaved grass	1.20	1.14	0.60	1.03
Fine-leaved grass	0.15	0.35	0.21	3.43
Grass stem and flower	1.75	0.86	0.36	0.32
Dicots	0.10	25.29	0.28	32.22
Juncus spp	5.34	2.02	33.39	0.66
Dead	0.13	0.18	0.57	0.68

Table E3.18

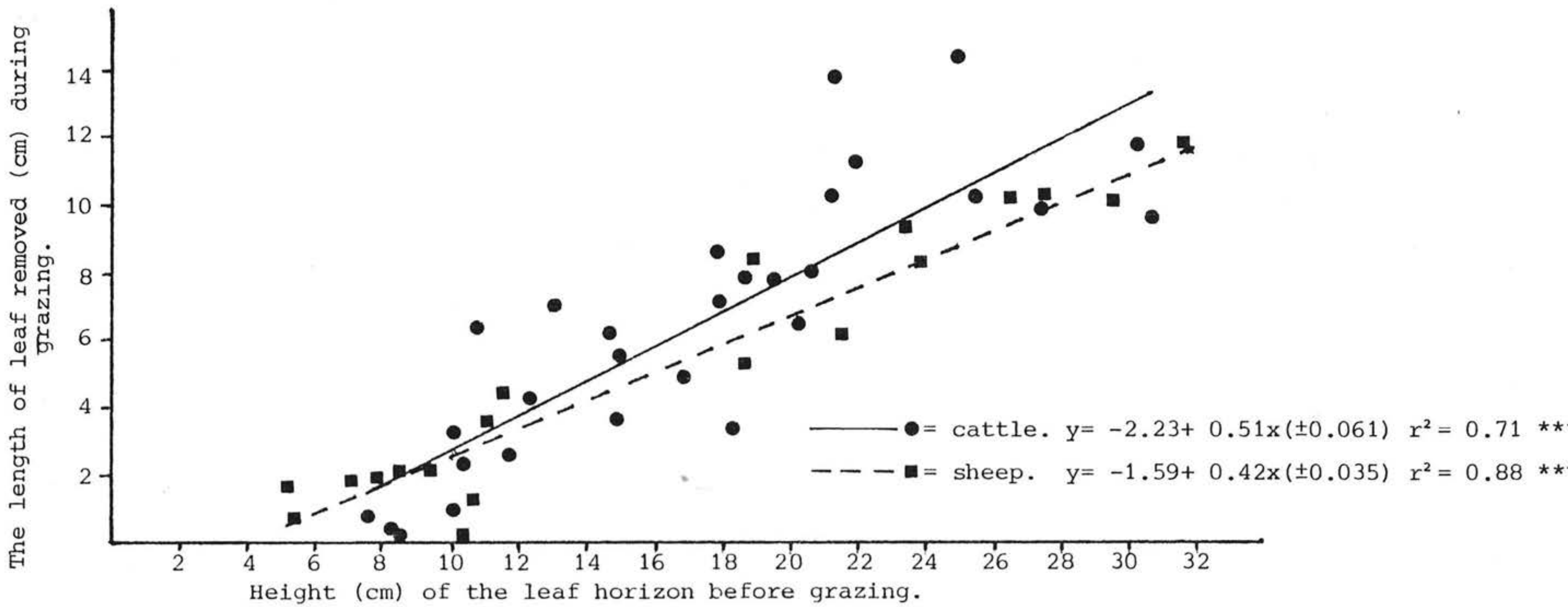
The mean height (cm ± SE) of the grass leaf horizon before and after grazing by the cattle and sheep in 1979 and 1980.

Sward and month of measurement	Cattle Pre-grazing	Cattle Post-grazing	Sheep Pre-grazing	Sheep Post-grazing
1979				
Nardus (May)				
Transect 1	10.8 ± 0.75	4.4 ± 0.24	9.4 ± 1.05	7.2 ± 0.23
2	7.6 ± 0.62	6.8 ± 0.62	(+)	
3	10.4 ± 0.61	8.1 ± 0.14	(+)	
4	12.4 ± 1.03	8.1 ± 0.49	(+)	
Molinia (June)				
Transect 1	18.3 ± 0.89	14.9 ± 0.25	23.5 ± 0.46	14.1 ± 0.23
2	25.6 ± 0.94	15.3 ± 0.40	27.8 ± 0.91	17.5 ± 0.25
3	20.3 ± 0.63	13.8 ± 0.13	19.0 ± 0.56	10.6 ± 0.15
4	21.3 ± 0.60	11.0 ± 0.29	(+)	
5	20.6 ± 0.69	12.5 ± 0.25	(+)	
6	22.5 ± 1.67	14.7 ± 0.44	(+)	
Ryegrass (July)				
Transect 1	22.0 ± 1.22	10.7 ± 0.16	26.6 ± 2.20	16.4 ± 0.20
2	19.6 ± 1.34	11.8 ± 0.14	18.7 ± 0.73	13.4 ± 0.28
3	14.7 ± 1.46	8.5 ± 0.11	29.6 ± 1.26	19.5 ± 0.35
4	17.9 ± 1.41	9.3 ± 0.72	21.6 ± 0.79	15.4 ± 0.26
5	25.0 ± 1.00	10.6 ± 0.19	23.9 ± 1.12	15.6 ± 0.24
6	18.7 ± 1.27	10.8 ± 0.48	(+)	
Molinia (August)				
Transect 1	30.7 ± 1.69	21.1 ± 0.35	31.7 ± 1.37	19.8 ± 0.16
2	30.3 ± 1.25	18.4 ± 0.15	(+)	
3	27.5 ± 1.32	17.5 ± 0.24	(+)	
Agrostis-Festuca (September)				
Transect 1	8.3 ± 0.55	2.9 ± 0.13	7.8 ± 0.32	5.9 ± 0.10
2	8.5 ± 0.40	8.2 ± 0.71	5.2 ± 0.51	4.5 ± 0.13
3	(+)		7.0 ± 0.40	5.1 ± 0.08
4	(+)		5.0 ± 0.43	3.3 ± 0.07
Nardus (October)				
Transect 1	11.8 ± 0.66	9.2 ± 0.08	11.5 ± 1.24	7.0 ± 0.15
2	10.1 ± 0.74	9.1 ± 0.07	10.4 ± 1.01	10.1 ± 0.21
3	14.9 ± 0.87	11.2 ± 0.12	13.4 ± 0.85	13.3 ± 0.25
4	15.0 ± 1.41	9.4 ± 0.09	10.7 ± 0.65	7.4 ± 0.09
1980				
Agrostis-Festuca (July)				
Transect 1	16.9 ± 0.47	12.0 ± 0.14	11.1 ± 1.08	7.5 ± 0.21
2	10.1 ± 0.67	6.8 ± 0.10	8.5 ± 0.65	6.4 ± 0.89
3	21.4 ± 2.68	7.6 ± 0.12	9.9 ± 0.44	7.0 ± 0.12
4	17.9 ± 1.08	10.7 ± 0.11	(+)	
5	13.1 ± 0.99	6.0 ± 0.15	(+)	

(+) No post-grazing records.

Figure E3.7.

The depth of the grazed leaf horizon regressed on the pregrazing leaf height.



The full number of records (6 per plot) were not always obtained because there were some problems in getting the animals, particularly the sheep, to graze. Figure E3.7 shows the relationships between the length of leaf removed and the pregrazing extended leaf height.

Principal component and regression analysis

Following the initial analysis of the data from the animal measurements the sward mean values from the following groups of variates were used in a correlation matrix (Appendix 4):

(1) The ingestive behaviour variates of both the cattle and the sheep. These variates consisted of OMD, HOMILW, intake per bite, rate of biting, grazing time and total bites per day.
(2) The diet composition variates, both as proportions and weights (g OM ingested per kg LW per day). These variates consisted of total green material, total grass leaf, broad-leaved grass leaf, fine-leaved grass leaf, total stem and flower, dicots, miscellaneous species, Juncus and total dead. (The weights of the components in the diet were obtained from the components of the diet as proportions of mean daily HOMILW).
(3) The sward composition variates, both as proportions and weights (kg/ha) with the same components as the diet composition variates.

Principal component analysis was then carried out on the sward and diet composition data in order that the large amount of information could be condensed into a smaller number of variates that not only provided an adequate description of the sward or the diet but could also be used in multiple regression analysis without the problems of interpretation arising due to inter-correlation of the x-variates. Both sets of diet and sward variates were used in

Table E3.19.1

The proportion of the variability explained and the eigenvectors calculated by principal component analysis from the proportion of herbage components in the diets of the cattle and sheep.

Proportions of components in the diets of the cattle and sheep

	Cattle			Sheep		
Principal components	1 (diet quality)	2 (grasslessness)	3 (stemlessness)	1 (diet quality)	2 (dicot vs grass)	3 (greenness)
Proportion of variability	0.6009	0.2147	0.1312	0.7308	0.1910	0.0519
Herbage components †	Eigenvectors					
Broad-leaved grass	0.5646	-0.2815	0.5807	0.6915	-0.4250	-0.1157
Fine-leaved grass	-0.5733	-0.3260	-0.2109	-0.6667	-0.2899	0.2464
Grass stem and flower	0.3582	-0.2563	-0.6185	0.1415	-0.0466	0.4954
Dicots	0.0229	-0.0839	-0.0981	0.1260	0.8544	0.0602
Miscellaneous	-0.0061	-0.0004	0.0122	-0.0158	-0.0541	-0.0005
Juncus	0.1172	0.8579	-0.1246	0.0223	0.0124	0.0209
Dead	-0.4582	0.0760	0.4588	-0.2020	0.0078	-0.8225

† Due to rounding errors the proportions of the individual components do not sum exactly to 1.0, and so the Eigenvectors do not sum to zero. This does not influence the interpretation of these results.

the analysis. However the values for total green material and total grass leaf were not included in the proportions analysis as both variates were derived from other variates in the data set. Tables E3.19.1 to E3.19.3 give the proportion of the variability accounted for by the principal components (PC) used and their eigenvectors. Decisions on the number of PC's to be used in regression analyses were made on the basis of the proportion of variability accounted for. PC's contributing less than 0.05 of the total variability were not used in further analyses.

Before regression analyses can be carried out the PC's which are to be used can be given appropriate names, and the principal component scores calculated from the eigenvectors are then used as the values for the named principal components in the later regression analyses. (See the section on statistical analyses). The scores are given in Appendix Tables E3.16.1 to E3.16.5. The following interpretations were given to the PC's used in later analyses.

(1) PC's from the proportions of herbage components in cattle diets (Table E3.19.1)

PC1 contrasts the combination of broad-leaved grass and stem with the combination of fine-leaved grass and dead material. This PC was called 'cattle diet quality', since both fine-leaved grass and dead were negatively correlated with the OMD of the cattle diet.

PC2 contrasts *Juncus* with fine-leaved grass. However the contrast appears to be more complex than this since both *Juncus* and dead are positive whilst all other variates are negative, and the dead component though small does appear to influence this PC. The importance of the dead material is highlighted when the scores for the PC are examined (Appendix Table E3.16.1). The score for the May 1979 Agrostis-Festuca site, in which there was no Juncus but a large amount of dead material, is higher than both 1979 Molinia swards in which there was little dead but large amounts of Juncus. The proportion of dead in the cattle diet on the May 1979 Agrostis-Festuca sward was very high (0.55) and thus dead appears to be contributing quite strongly to this PC. It is probable that this PC reflects a lack of green grass in the diet since the eigenvalues of the broad-leaved grass and grass stem and flower are only slightly lower than the fine-leaved grass. This PC was therefore called 'grasslessness'.

PC3 contrasts the combination of broad-leaved grass and dead with grass stem and flower. This PC was therefore called 'stemlessness'.

(2) PC's from the proportions of herbage components in the sheep diet (Table E3.19.1)

PC1 contrasts broad-leaved grass with fine-leaved grass and as fine-leaved grass and dead are both negative fectors and since both are negatively correlated with sheep diet OMD it was decided to call this component 'sheep diet quality'.

PC2 contrasts dicots with broad-leaved grass and to a smaller extent fine-leaved grass. The selection ratios (Tables E3.12.1 to E3.17.3) suggest that sheep select rather less for dicots than they do for broad-leaved grass, and since broad-leaved grass, fine-leaved grass and grass stem and flower are all negative vectors this component appears to represent 'dicot versus grass'.

PC3 contrasts grass stem and flower and fine-leaved grass with dead. Since dead is the most important vector, though negative, it does not seem too unreasonable to suggest that the contrast is green versus dead. This component was therefore called 'greenness'.

Table E3.19.2

The proportion of the variability explained, and the eigenvectors calculated by principal component analysis from the weights of the herbage components in the diets of the cattle and sheep.

Weights of herbage components in the diet of the cattle and sheep

	Cattle			Sheep	
Principal components	1 (low quality diet)	2 (grassless-ness)	3 (leafless-ness)	1 (low quality diet)	2 (broad leaf vs dicot selection)
Proportion of variability	0.5959	0.2129	0.1375	0.6475	0.2481
Herbage components			Eigenvectors		
Broad-leaved grass	-0.6035	-0.1418	-0.5751	-0.6351	0.3085
Fine-leaved grass	0.5760	-0.4474	0.0225	0.6671	-0.1167
Grass stem and flower	-0.3531	-0.6042	0.6033	-0.1308	-0.0096
Dicots	-0.0256	-0.1560	0.0478	-0.3132	-0.9366
Miscellaneous	0.0036	-0.0003	-0.0168	0.0154	0.0359
Juncus	-0.1160	0.6213	0.5063	-0.0291	0.0066
Dead	0.4064	0.0661	-0.2141	0.1882	-0.1125

It can be noted that the contrasts are somewhat simpler in the sheep than in the cattle and as such may reflect a greater degree of selection for some and avoidance of other components by the sheep.

(3) PC's from the weight of herbage components ingested by cattle (gOM/kgLW/day) (Table E3.19.2)

PC1 contrasts fine-leaved grass and dead with broad-leaved grass and stem. This is the same contrast as for the proportions but with the sign on the eigenvectors reversed, so it was called 'cattle low-quality diet'.

PC2 contrasts Juncus with the combination of stem and fine-leaved grass and is somewhat similar to PC2 'grasslessness' from the proportions of herbage components in the diet. Again the high positive score for the May 1979 Agrostis-Festuca sward (Appendix Table E3.16.3) is a result of low weights of grass leaf and stem which has resulted in this sward having a higher score for this PC than three of the four Molinia swards.

PC3 contrasts grass stem and flower and Juncus with broad-leaved grass. On the face of it the contrast appears to represent non-leaf components on the one hand and leafy components on the other. However since Juncus and grass stems are the tallest components in the sward it may be a contrast between the taller and the shorter items. However, examination of the correlation matrix (Appendix 4) reveals that the weight of Juncus in the diet is negatively correlated ($P < 0.01$) with the weight of total grass leaf in the diet; this adds weight to the first interpretation that this PC contrasts non-leafy with leafy components of the diet and so it was called 'leaflessness' as in the case of diet proportions.

(4) PC's from the weights of herbage components ingested by the sheep (gOM/kgLW/day) (Table E3.19.2)

PC1 contrasts fine-leaved grass with broad-leaved grass. As with the cattle this PC is the same as that from the proportions of

Table E3.19.3

The proportion of the variability explained and the eigenvectors calculated by principal component analysis from the proportions and weights of the herbage components in the sward.

Proportions and weights of herbage components in the sward

Principal components	Proportions 1 (low sward quality)	Proportions 2 (opportunity for selection)	Weights 1 (sward deadness)
Proportion of variability	0.8827	0.0723	0.9755
Herbage components	Eigenvectors		
Broad-leaved grass	-0.7647	-0.0587	-0.0929
Fine-leaved grass	0.4144	0.5494	0.1471
Grass stem and flower	-0.1898	-0.0914	0.0842
Dicots	0.1118	0.3548	0.0273
Miscellaneous	0.0050	0.0347	-0.0052
Juncus	-0.0173	-0.0129	-0.0006
Dead	0.4413	-0.7477	0.9808

herbage components in the diet but with the signs reversed. Thus it was called 'sheep low-quality diet'.

PC2 contrasts diets high in broad-leaved grass with those high in dicots, and was called 'broad leaf versus dicot selection'.

(5) Principal components from the proportions of herbage components in the sward (Table E3.19.3)

PC1 contrasts the combination of dead and fine-leaved grass with broad-leaved grass and so was called 'low sward quality', since both cattle and sheep diet OMD were negatively correlated with total dead and fine-leaved grass proportions and positively correlated with broad-leaved grass proportion in the sward (Appendix 4).

PC2 contrasts the combination of fine-leaved grass and dicots in the sward with dead herbage. Since animals select for green components and avoid dead herbage, swards which show such a contrast could result in the expression of diet selection. This PC was thus called 'opportunity for selection'.

(6) PC's from the weight of herbage components in the sward (kg/ha) (Table E3.19.3)

PC1 had only one eigenvector of any importance, that of dead herbage and so the component was called 'sward deadness'. This eigenvector contributed almost all of the variation in component weight.

The new variates were then used as the independent variables in a series of regression analyses in which the dependent variables were either the cattle and sheep ingestive variates or the proportions of herbage components in the diets of the cattle and sheep. The results of the regressions are given in Tables E3.20.1 to E3.20.6. Each table gives the value for the intercept and the slope, the standard error for the slope and the r^2 value for the simple

Table E3.20.1

The relationships between cattle ingestive variates and PC1 and PC2 derived from the proportions of herbage components in the sward.

Ingestive variates y	PC1 'low sward quality'	PC2 'opportunity for selection'	r^2 for multiple regression
OMD	70.94-12.19x(±3.555) r^2=0.55**	+	0.55**
HOMILW	+	20.60+16.91x(±11.400) r^2 = 0.15NS	0.18 NS
Intake per bite	+	0.66+0.94x(±0.691) r^2=0.13NS	0.13 NS
Rate of biting	56.43+9.55x(±8.91) r^2=0.09NS	+	0.09 NS
Grazing time	+	579.8-267.8x(±226.01) r^2=0.10NS	0.11 NS
Total bites per day	+	+	

+ Residual variance exceeds variance of y-variate regression equations on each PC in turn, and also the r^2 value for the multiple regression. No significant regressions resulted from the regressions of the cattle and sheep ingestive variates on the only important PC derived from the weight of herbage components in the sward, 'sward deadness', and so no results of sward component weight analyses are shown.

When the cattle and sheep ingestive variates were regressed on to the variates derived from the principal components of the proportions of herbage components in the sward (Tables E.3.20.1 and E3.20.2), simple linear regressions of 'low sward quality' explained significant proportions of the variability in cattle diet OMD and in sheep grazing time and diet OMD (Figures E3.8 and E3.9) whilst simple linear regression on 'opportunity for selection' explained a significant proportion of sheep HOMILW (Figure E3.10). The multiple regressions on 'low sward quality' and 'opportunity for selection' did not significantly reduce the residual variation in these variates.

The variates calculated from the PCs of the proportions of herbage components in the diets of the cattle and sheep provided satisfactory linear explanations of the cattle intakes, rates of biting, weights per bite and diet OMD (Table E3.20.3) and of the sheep intakes, grazing times and diet OMD (Table E3.20.4). The regression of cattle rate of biting was improved by the use of all three independent variates even though cattle 'diet quality' and 'grasslessness' did not themselves provide significant solutions. Sheep diet OMD was better explained by the multiple regression involving all three independent variates than by 'dicot vs grass', and similarly grazing time was better explained by the multiple regression than by 'diet quality'. Since none of the significant regressions were the same for both cattle and sheep and since the

Table E3.20.2

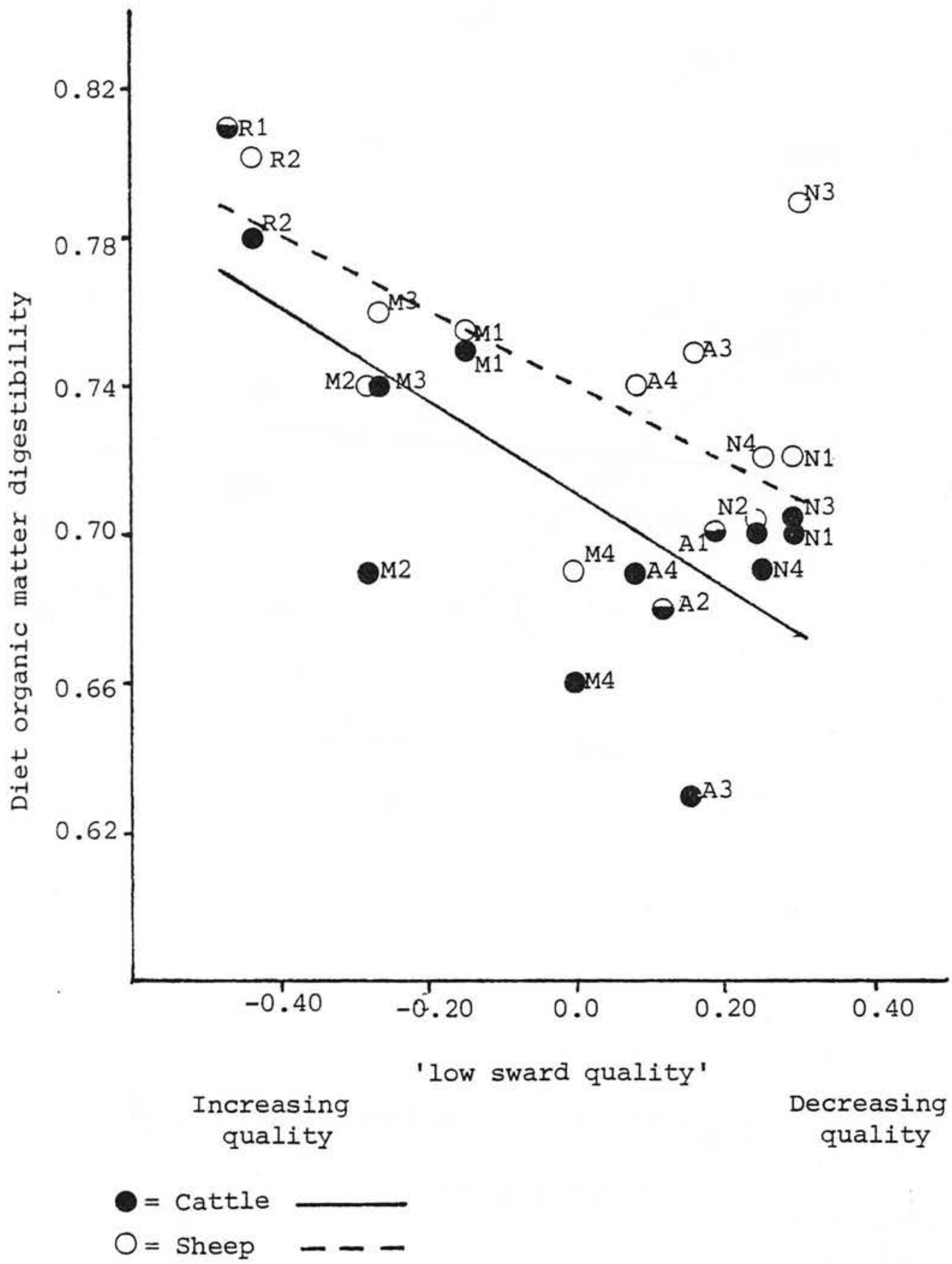
The relationships between sheep ingestive variates and PC1 and PC2 derived from the proportions of herbage components in the swards

Ingestive variates y	PC1 'low sward quality'	PC2 'opportunity for selection'	r^2 for multiple regression
OMD	73.86-9.70x(±3.653) r^2 = 0.37*	+	0.37 NS
HOMILW	+	27.28+35.61x(±15.091) r^2=0.32*	0.37 NS
Intake per bite		0.96 + 1.76x(± 1.079) r^2=0.18NS	0.22 NS
Rate of biting	+	+	0.04 NS
Grazing time	566.5+179.3x(±58.39) r^2=0.44*	+	0.49 *
Total bites per day	30502.8+12890.7x(±8123.1) r^2=0.17NS	+	0.20 NS

+ = Residual variance exceeds variance of y-variate.

Figure E3.8

The relationship between the OMD of the diet of the cattle and sheep and the principal component 'low sward quality'



R1, R2, A1, A2, etc. refer to the swards and dates of measurement. For explanation see Glossary.

Figure E3.9

The relationship between the grazing times of the cattle and sheep and the principal component 'low sward quality'

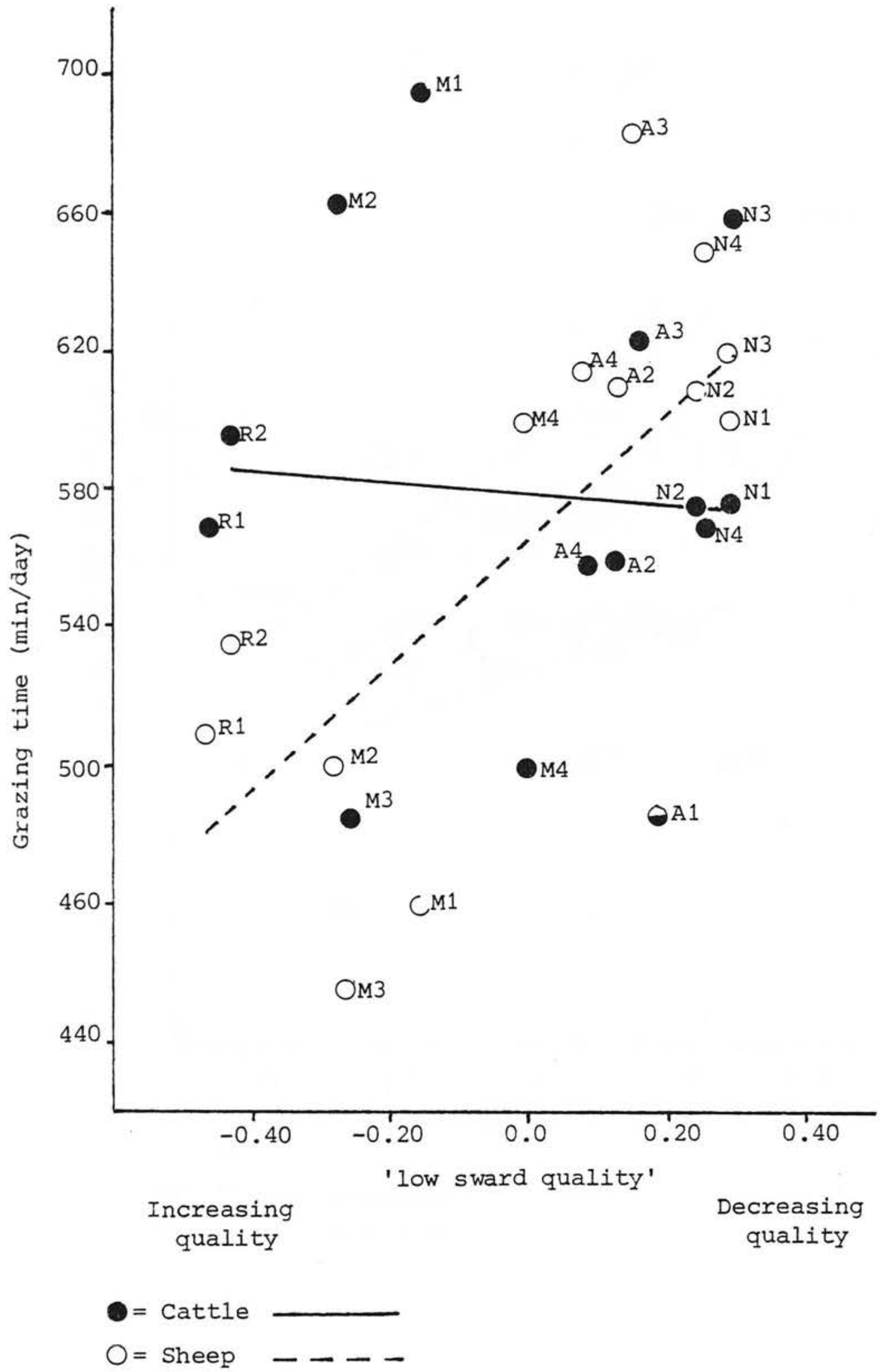
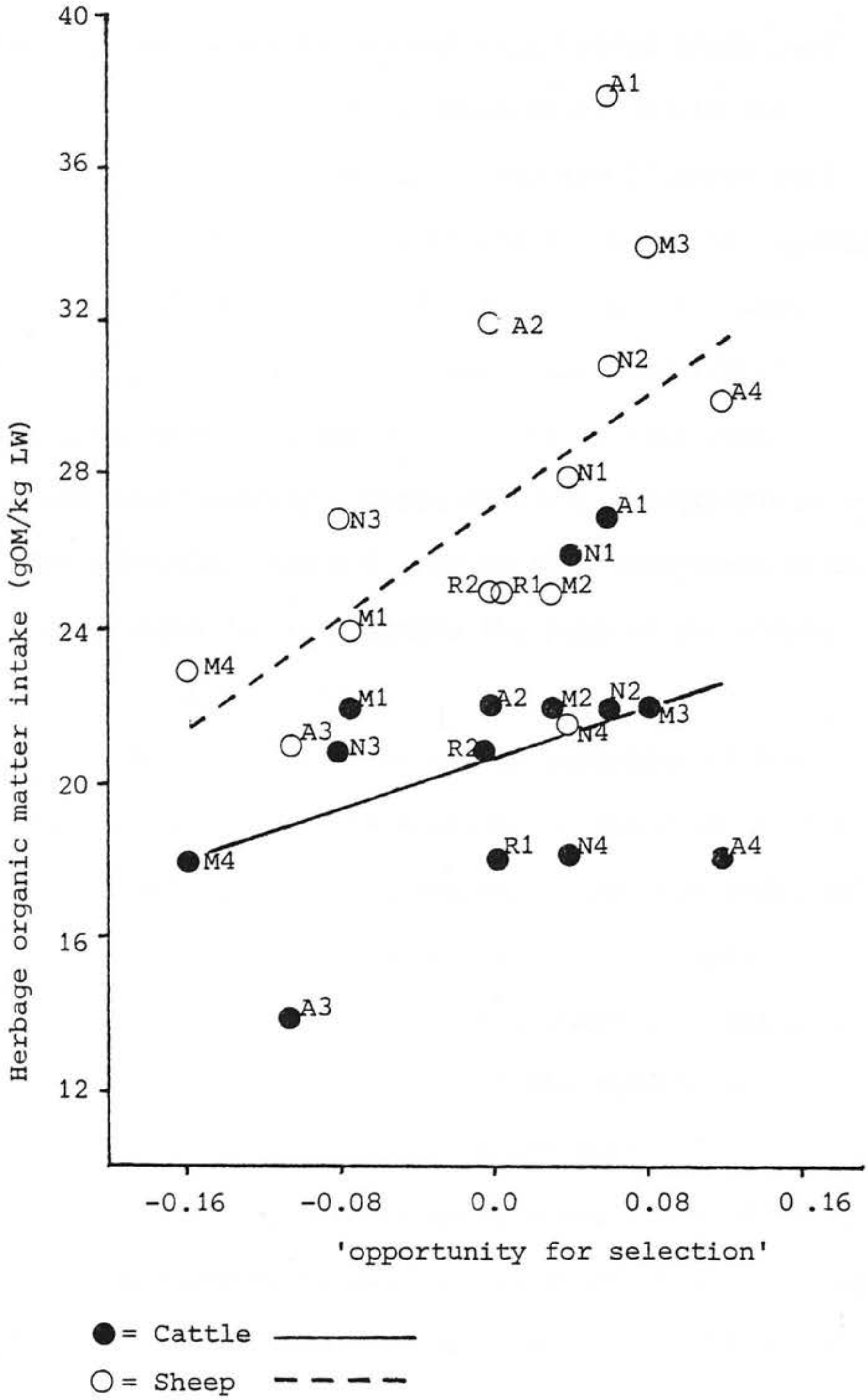


Figure E3.10

The relationship between the herbage organic matter intake of the cattle and sheep and the principal component 'opportunity for selection



PC's had different interpretations (Tables E3.20.3 and E3.20.4) no regressions are illustrated.

Simple regressions on 'low sward quality' derived from the proportions of herbage components in the sward explained significant proportions of the variation in the proportions of the components total green, broad-leaved and fine-leaved grass leaf in the cattle diet (Table E3.20.5) (Figures E3.11, E3.12 and E3.13), but only the regression of the proportion of grass leaf on 'opportunity for selection' was significant. Multiple regressions did not improve the fit of any of the regressions. Sheep dietary components total green, broad-leaved and fine-leaved grass leaf and total stem gave significant regressions when regressed on 'low sward quality' (Table E3.20.6). Regressions on 'opportunity for selection' did not produce any significant fits, and multiple regressions did not improve the fits of the simple regressions on 'low sward quality'.

The causes of the different behavioural responses of the cattle and sheep to the swards were examined by using the cattle-sheep differences (C-S) in ingestive behaviour and diet composition as dependent variates and regressing them on the principal components derived from the proportions of herbage components in the sward. Tables E3.21.1 and E3.21.2 give the results of the regressions. Dead material in the diet is not included in Table E3.21.2 since it is the converse of total green. C-S differences in intake, OMD, weight per bite, rate of biting and bites per day were not explained by the regressions on 'low sward quality' or 'opportunity for selection' (Table E3.21.1). Some of the variation in the difference in grazing time was explained by 'low sward quality' (Figure E3.14). Differences in the proportions of total

Table E3.20.3

The relationships between the cattle ingestive variates and PC's 1, 2 and 3 derived from the proportions of herbage components in the cattle extrusa.

Ingestive variates y	PC1 'diet quality'	PC2 'grasslessness'	PC3 'stemlessness'	r^2 for multiple regression
OMD	70.94+11.42x(±3.438) r^2 = 0.48**	70.94-12.22x(±7.146) r^2 = 0.20 NS	+	0.68 **
HOMILW	+	20.60-6.53x (±5.309) r^2 = 0.11 NS	20.60-16.81x(±5.326) r^2 = 0.45 **	0.59 *
Intake per bite	0.66+0.22x (±0.192) r^2 = 0.10 NS	+	0.66-0.95x (±0.334) r^2 = 0.40 *	0.50 NS
Rate of biting	56.43-15.44x(±7.646) r^2 = 0.25 NS	56.43-18.98x(±13.757) r^2 = 0.14NS	56.43+39.53x(±15.116) r^2 = 0.36 *	0.75 **
Grazing time	+	+	+	
Total bites per day	32882.0-9847.8x(±6443.77) r^2 =0.16NS	32882.0-15036.3x(±10955.80) r^2 = 0.14NS	32882.0+23177.7x(±13506.50) r^2 =0.20NS	0.49 NS

+ = Residual variance exceeds variance of y-variate

Table E3.20.4

The relationships between the sheep ingestive variates and PC's 1, 2 and 3 derived from the proportions of herbage components in the sheep extrusa

Ingestive variates y	PC1 'diet quality'	PC2 'dicot vs grass'	PC3 'greenness'	r^2 for multiple regression
OMD	73.86+7.60x (±3.910) r^2 = 0.24NS	73.86-16.66x (±7.331) r^2 = 0.30*	73.86+27.77x (±14.791) r^2 = 0.23NS	0.77**
HOMILW	+	27.28-24.52x (±7.004) r^2 = 0.51**	+	0.54*
Intake per bite	0.96+0.39x (±0.313) r^2 = 0.11NS	0.96+1.24x (±0.543) r^2 = 0.30*	0.96+1.69x (±1.147) r^2 = 0.15NS	0.57*
Rate of biting	+	+	53.21-41.65x (±34.807) r^2 = 0.11NS	+
Grazing time	566.6-203.8x (±48.11) r^2 = 0.60**	566.6-148.6x (±142.30) r^2 = 0.08NS	566.6-307.41x (±271.02) r^2 = 0.10NS	0.78***
Total bites per day	30503.0-13214.0x(±7821.46) r^2 = 0.19NS	+	30503.0-42057.1x(±30315.1) r^2 = 0.14NS	0.40NS

+ = Residual variance exceeds variance of y-variate

Figure E3.11

The relationship between the proportion of total green herbage in the diets of the cattle and sheep and the principal component ' low sward quality'

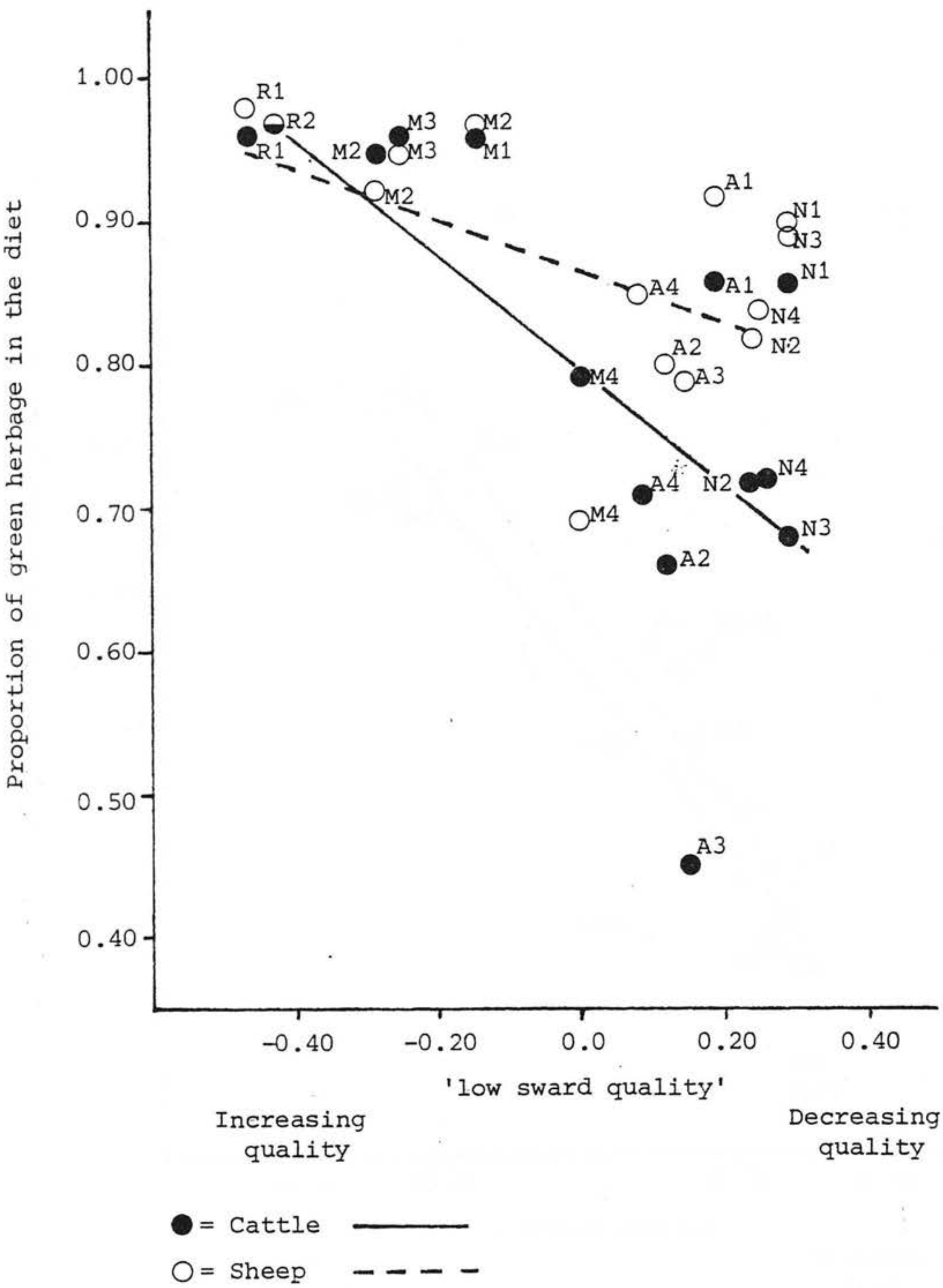


Figure E3.12

The relationship between the proportion of broad-leaved grass leaf in the diets of the cattle and sheep and the principal component 'low sward quality'

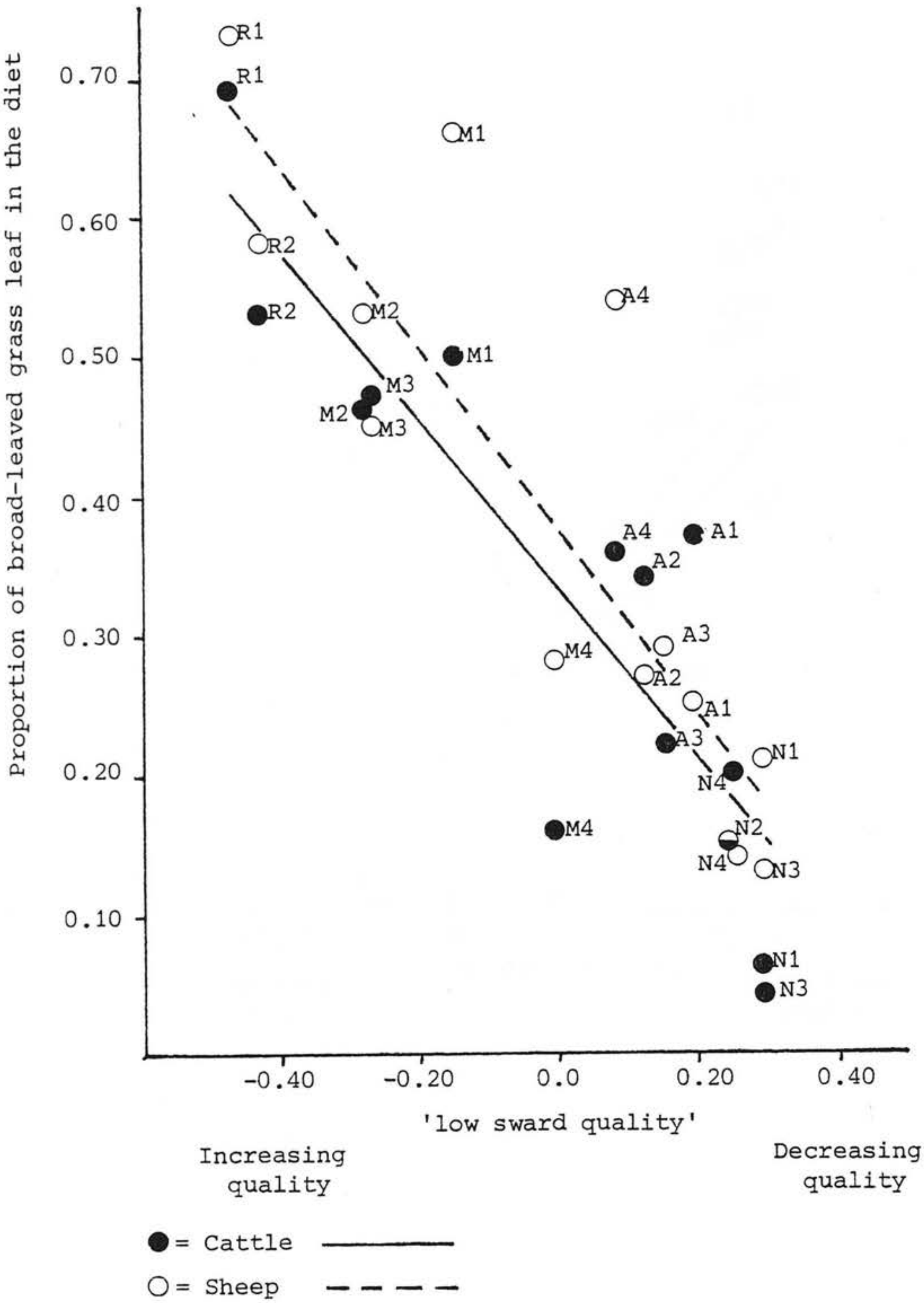
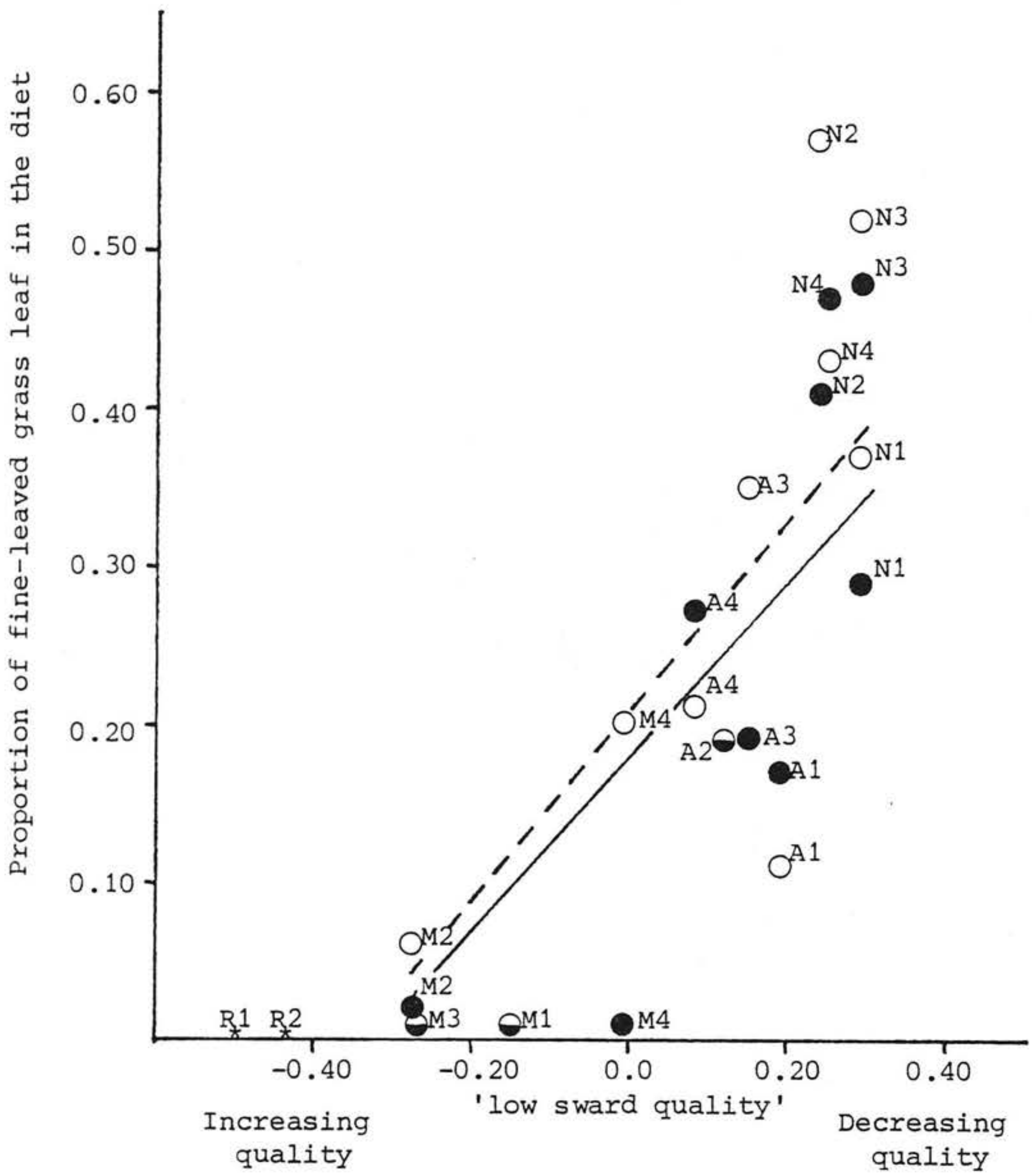


Figure E3.13

The relationship between the proportion of fine-leaved grass leaf in the diets of the cattle and sheep and the principal component 'low sward quality'



= Cattle

= Sheep

Table E3.20.5

The relationships between the proportions of herbage components in the cattle diets and PC's 1 and 2 derived from the proportions of herbage components in the swards.

Components in the diet y	PC1 'low sward quality'	PC2 'opportunity for selection'	r^2 for multiple regression
Total green material	0.80-0.39x(±0.117) r^2=0.48**	+	0.55*
Total grass leaf	+	0.51 + 0.97x(±0.409) r^2=0.32*	0.33NS
Broad-leaved grass	0.33-0.61x(±0.092) r^2=0.79***	+	0.83***
Fine-leaved grass	0.18+0.56x(±0.104) r^2=0.71***	+	0.74***
Total stem	0.18-0.27x(±0.130) r^2=0.27 NS	+	0.32NS
Dicots	+	+	+
Miscellaneous	+	+	+
Juncus	+	0.07 - 1.03x(± 0.482) r^2 = 0.27	0.31NS

+ = Residual variance exceeds variance of y-variate

Table E3.20.6

The relationships between the proportions of herbage components in the sheep diets and PC's 1 and 2 derived from the proportions of herbage components in the swards.

Components in the diet y	PC1 'low sward quality'	PC2 'opportunity for selection'	r^2 for multiple regression
Total green material	0.87-0.18x (±0.074) r^2 = 0.33*	0.87+0.40x (±0.292) r^2 = 0.14 NS	0.47 *
Total grass leaf	+	+	+
Broad-leaved grass	0.37-0.66x (±0.103) r^2 = 0.77***	+	0.78***
Fine-leaved grass	0.21+0.60x (±0.107) r^2 = 0.72***	+	0.73***
Total stem	0.09-0.15x (±0.052) r^2 = 0.40*	+	0.41 NS
Dicots	0.16-0.15x (±0.143) r^2 = 0.08 NS	+	+
Miscellaneous	0.01+0.02x (±0.015) r^2 = 0.14 NS	+	+
Juncus	0.01+0.02x (±0.017) r^2 = 0.13 NS	+	+

+ = Residual variance exceeds variance of y-variate.

Table E3.21.1

The relationships between the cattle-sheep differences (C-S) in ingestive variates and PC's 1 and 2 derived from the proportions of herbage components in the sward.

C-S ingestive variates Y	PC1 'low sward quality'	PC2 'opportunity for selection'	r^2 for multiple regression
OMD	+	$-2.92+16.15x$ (± 11.559) $r^2 = 0.14$ NS	0.18 NS
HOMILW	+	$-6.68-18.70x$ (± 12.315) $r^2 = 0.16$ NS	0.19 NS
Intake per bite	$-0.30+0.24x$ (± 0.177) $r^2 = 0.14$ NS	$-0.30-0.82x$ (± 0.622) $r^2 = 0.13$ NS	0.26 NS
Rate of biting	+	+	+
Grazing time	$13.1-193.6x$ (± 82.79) $r^2 = 0.31$*	+	0.31 NS
Total bites per day	$2379.1-8005.7x$ (± 6321.7) $r^2 = 0.12$NS	+	+

+ = Residual variance exceeds variance of Y-variate.

Table E3.21.2

The relationships between the cattle-sheep differences (C-S) in the proportions of herbage components in their diets and PC's 1 and 2 derived from proportions of components in the sward.

C-S diet variates Y	PC1 'low sward quality'	PC2 'opportunity for selection'	r^2 for multiple regression
Total green material	-0.07-0.21x (±0.097) r^2=0.29*	+	0.29 NS
Total grass leaf	+	-0.11+0.95x (±0.400) r^2 = 0.32*	0.35 NS
Broad-leaved grass	+	+	+
Fine-leaved grass	+	-0.03+0.62x (±0.064) r^2 = 0.40*	0.42*
Total stem	0.09-0.13x (±0.105) r^2=0.11NS	0.09+0.51x (±0.359) r^2 = 0.14NS	0.25 NS
Dicots	-0.13+0.14x (±0.117) r^2=0.11NS	+	0.16 NS
Miscellaneous	+	+	+
Juncus	+	0.06-1.05x (±0.455) r^2 = 0.31*	0.33 NS

Figure E3.14

The relationship between the C-S difference in grazing time and the principal component 'low sward quality'

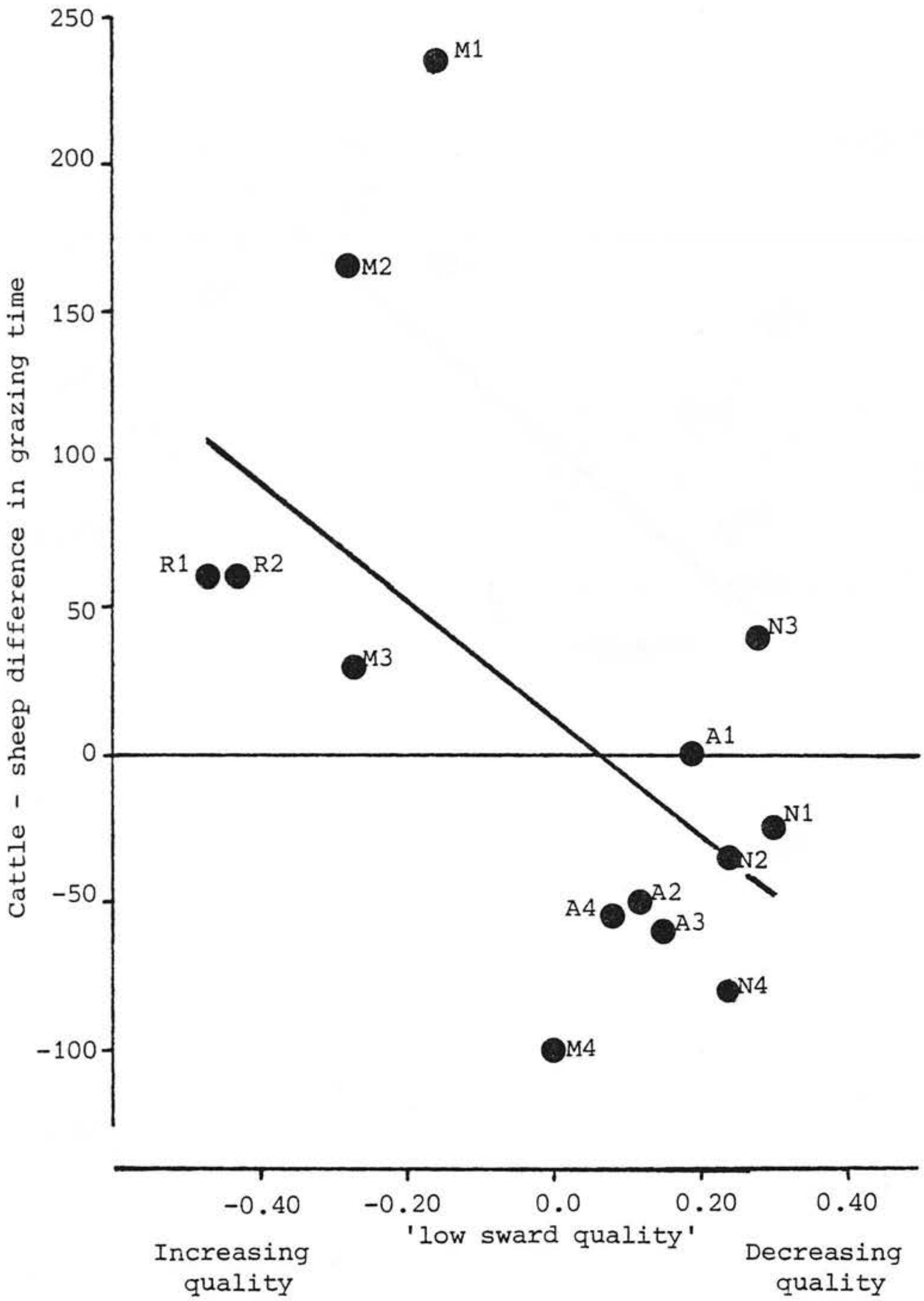


Figure E3.15

The relationship between the C-S difference in the proportion of total green herbage in the diet and the principal component 'low sward quality'

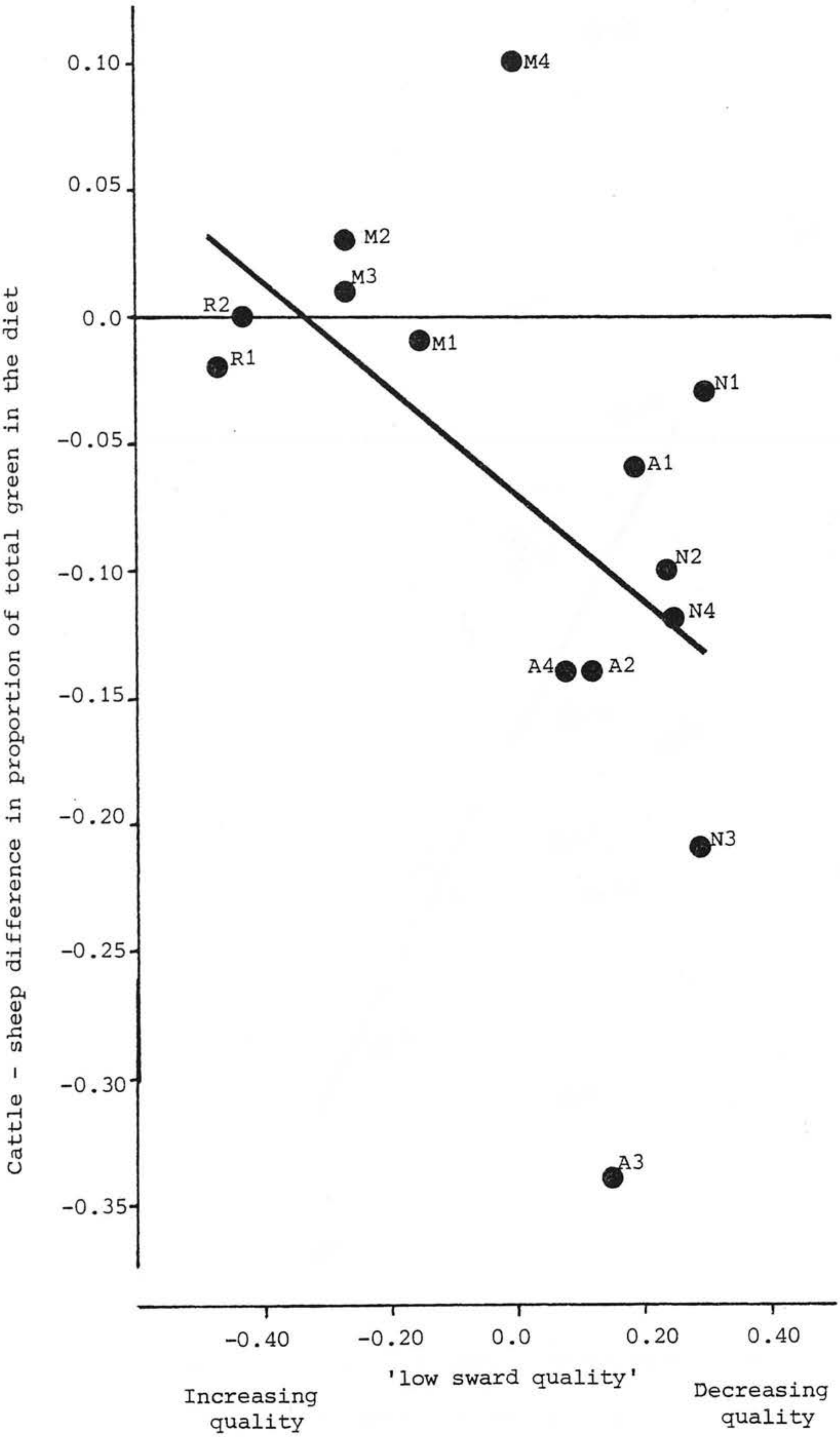


Figure E3.16

The relationship between C-S differences in the proportion of total grass leaf in the diet and the principal component 'opportunity for selection'

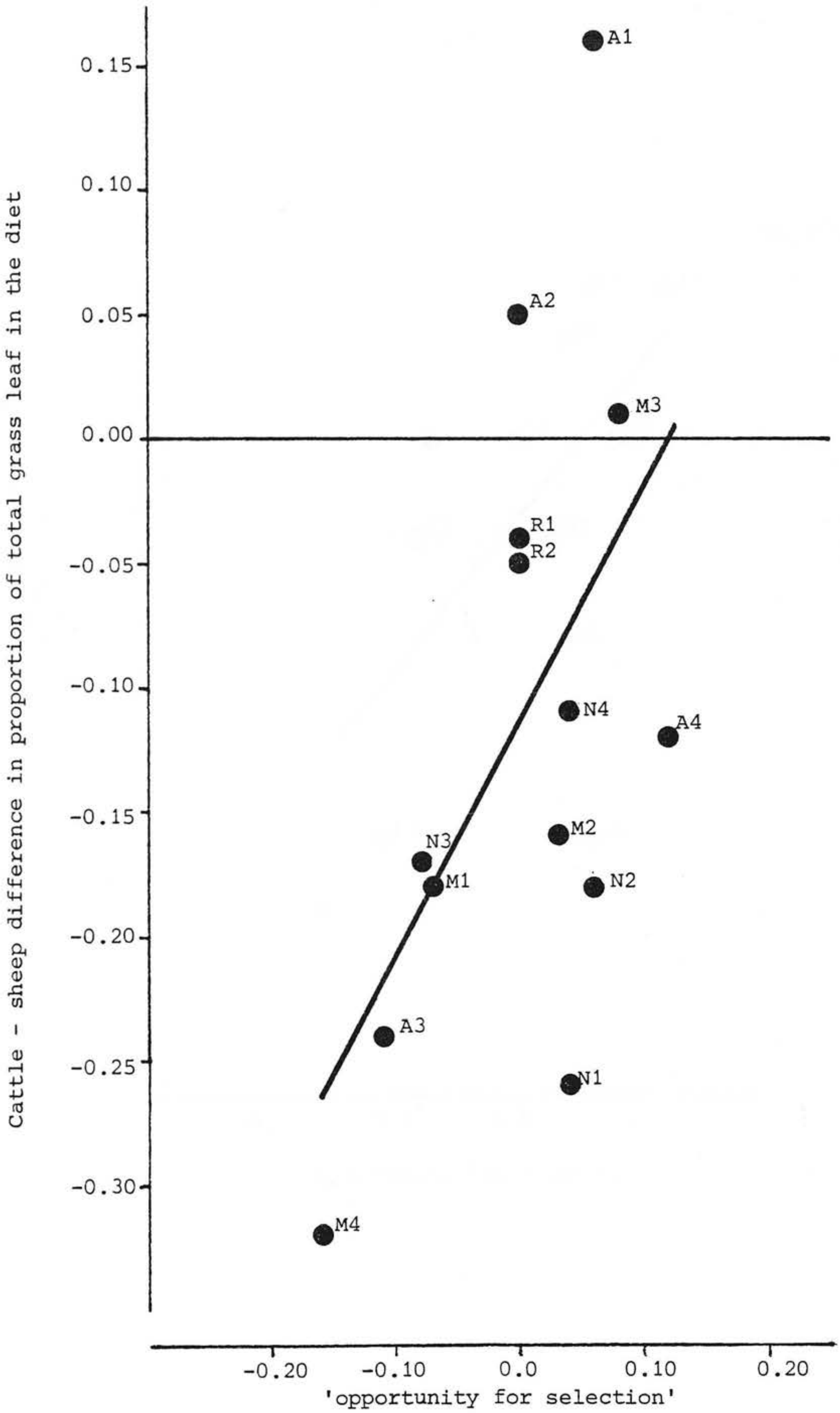


Figure E3.17

The relationship between the C-S difference in the proportion of fine-leaved grass leaf in the diet and the principal component 'opportunity for selection'

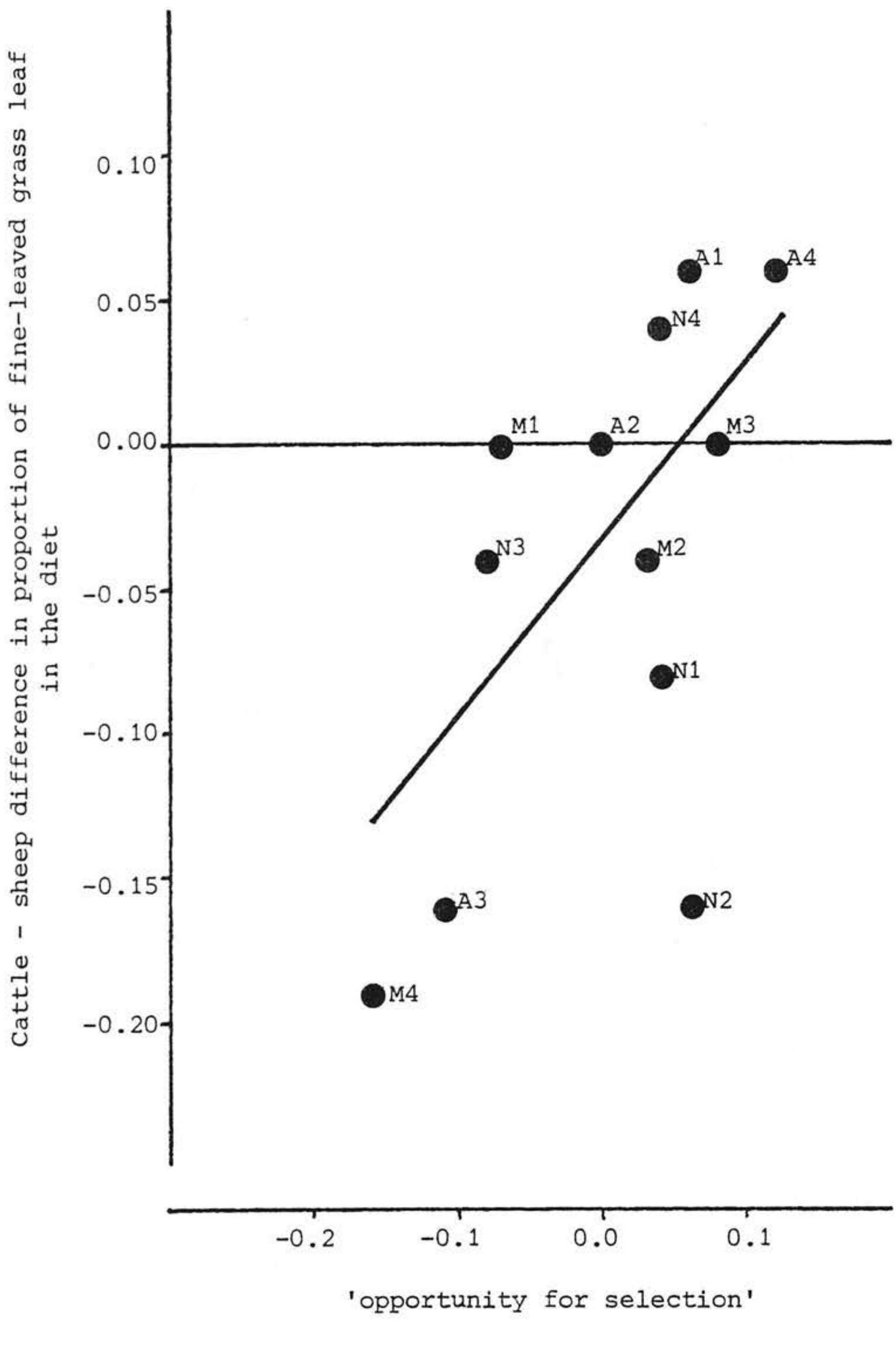


Table E3.22

The relationships between the cattle and sheep ingestive variates (y) and sward height (x).

Cattle

OMD	Residual variance exceeds variance of y-variate	
HOMILW	17.3 + 0.25x (±0.158)	r^2 = 0.17 NS
Intake per bite	0.36 + 0.02x (±0.008)	r^2 = 0.42*
Rate of biting	72.7 - 1.27x (±0.275)	r^2 = 0.64***
Grazing time	623.1 - 3.38x (±3.208)	r^2 = 0.08 NS
Total daily bites	44913.7 - 938.4x (±243.40)	r^2 = 0.55**

Sheep

OMD	78.3 - 0.35x (±0.202)	r^2 = 0.19 NS
HOMILW	Residual variance exceeds variance of y-variate	
Intake per bite	0.51 + 0.03x (±0.013)	r^2 = 0.37*
Rate of biting	69.0 - 1.23x (±0.343)	r^2 = 0.52**
Grazing time	648.9 - 6.41x (±3.348)	r^2 = 0.23 NS
Total daily bites	44396.7 - 1083.6x (±306.75)	r^2 = 0.51**

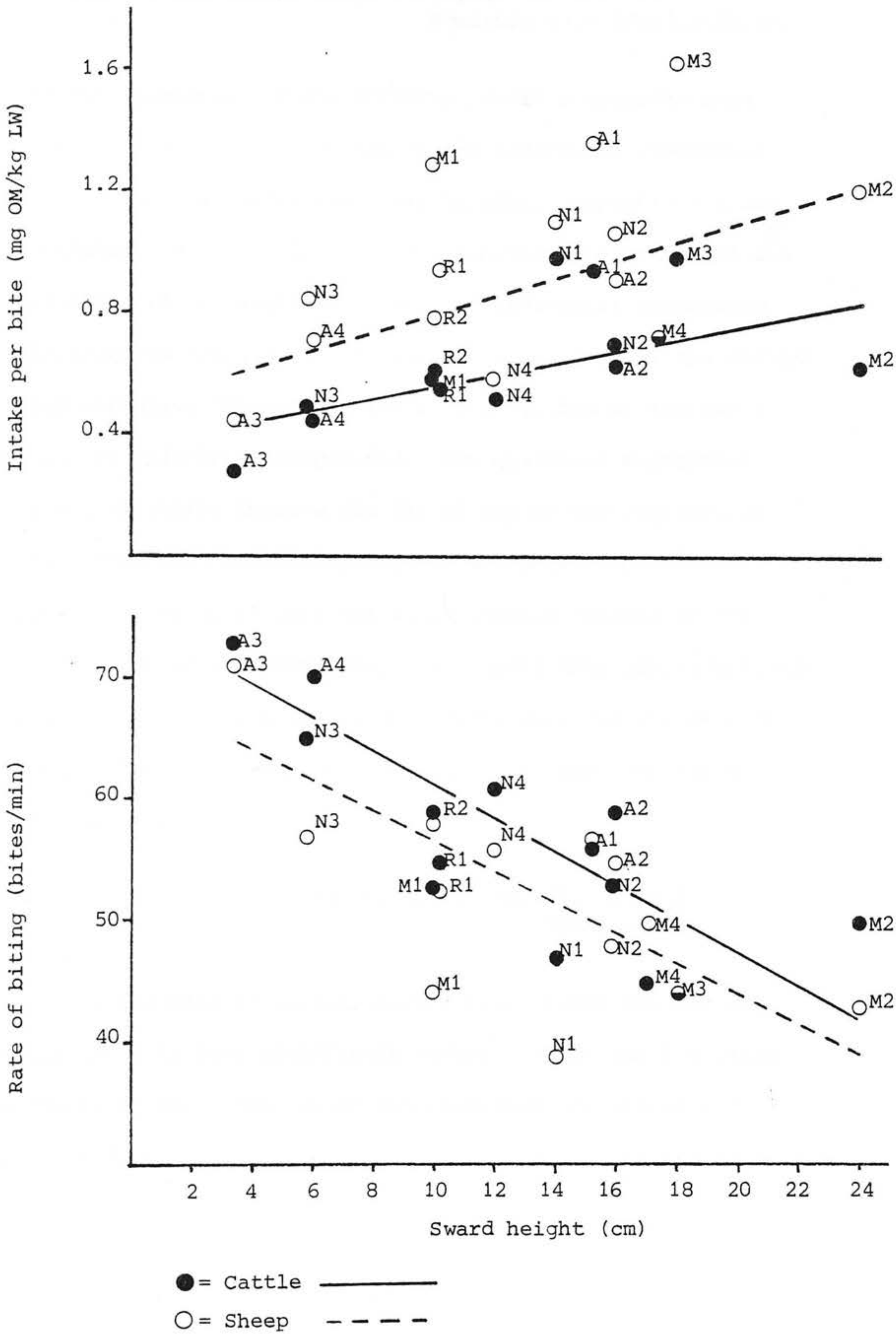
green, grass leaf, fine-leaved grass and Juncus in the diets had some of the variation explained by the regressions on 'low sward quality' or 'opportunity for selection' (Table E3.21.2) and Figures E3.15, E3.16 and E3.17). The relationship between Juncus in the diet and 'opportunity for selection' is not illustrated since Juncus only occurred in the diets of the animals grazing the Molinia swards.

The responses of the animals to sward variables which had not been included in the principal component analysis were examined in a further series of regression analyses. The variables were herbage mass and sward height, the bulk densities of the sward components and the leaf/stem ratio. The animal variables used as the dependent variates were OMD, HOMILW, intake per bite, rate of biting, grazing time and total daily bites. Analyses were carried out separately for cattle and sheep and the differences between the cattle and sheep (C-S) with the mean values of each x and y variate on each sward being used.

Neither linear nor quadratic regressions of the animal variates on herbage mass were significant. When the animal variates were regressed on sward height the only significant linear regressions were intake per bite (cattle $P < 0.05$; sheep $P < 0.05$), rate of biting (cattle $P < 0.001$; sheep $P < 0.01$) and total daily bites (cattle $P < 0.01$; sheep $P < 0.01$). Though the quadratic expression gave a better fit for most of the regressions the improvement was never significant. Table E3.22 gives the linear expression of the regressions of the cattle and sheep ingestive variates on sward height. Figure E3.18 shows the relationships between both intake per bite and rate of biting and sward height.

Figure E3.18

The relationships between cattle and sheep intakes per bite (mg OM/kgLW) and rates of biting (bites per minute), and sward height



There were no significant regressions of the C-S ingestive behaviour variates on sward height except for the difference in OMD of the diet selected. The regression equation was:

$$Y = -7.42 + 0.35x \text{ (sward height)} (\pm 0.143) \quad R^2 = 0.33^*$$

Equation E3.1 (Figure E3.19)

The bulk densities of the different sward components were calculated by dividing the weights of the individual components in the swards by the respective sward heights. Appendix 4 shows the correlations between the ingestive behaviour variates and the bulk densities of the whole sward and the individual components. Table E3.23 gives the significant linear regressions of the cattle and sheep ingestive variates on the bulk densities of the whole sward and the individual components. The quadratic expression did not significantly improve the fit of any of the regressions.

The differences between the cattle and sheep ingestive behaviour variates (C-S) were not significantly related to the densities of any of the sward components apart from the significant negative relationship between the OMD difference and the density of the miscellaneous component in the swards. The regression equation was as follows:

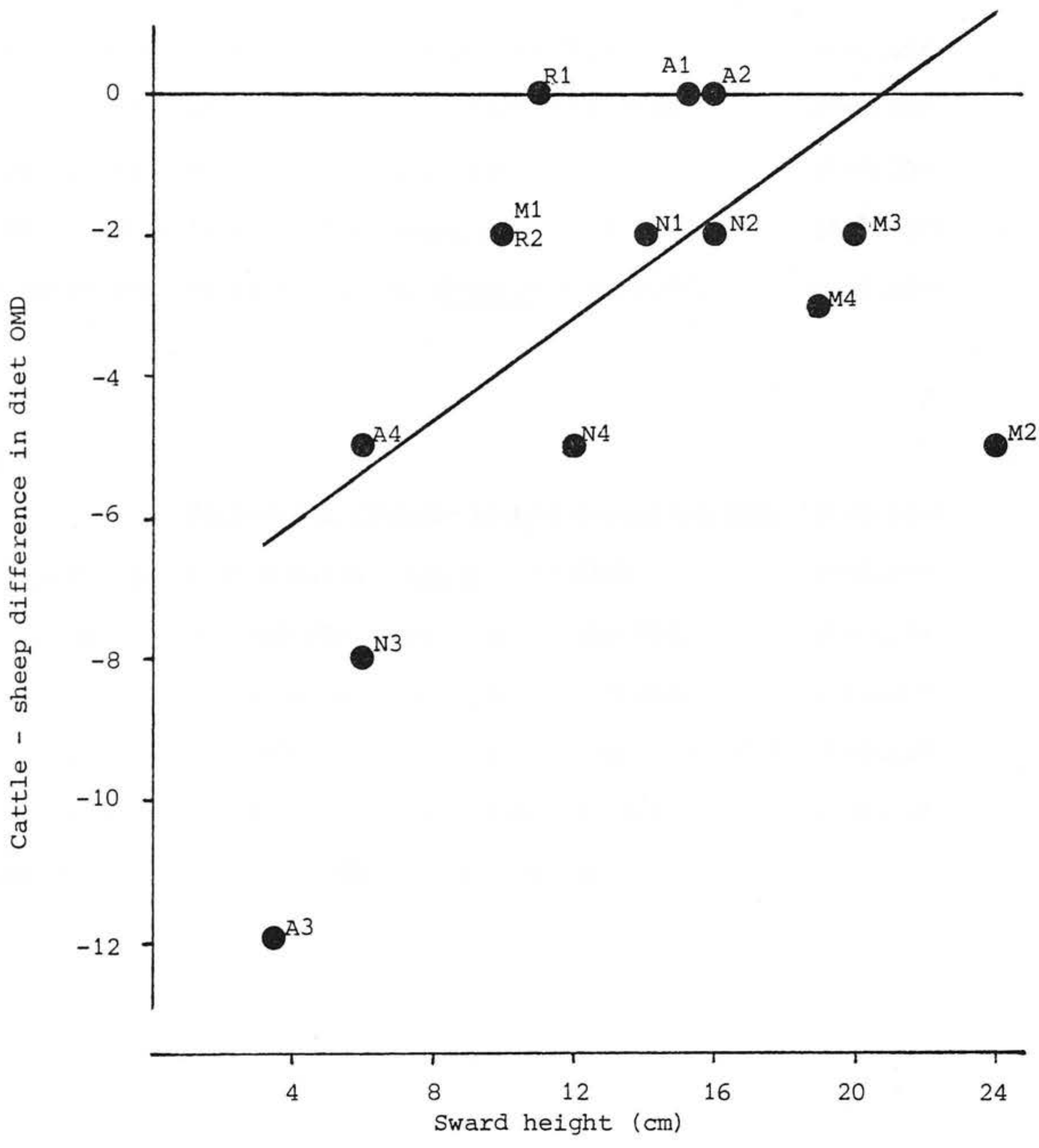
$$\text{C-S OMD} = -0.93 - 0.35 \text{ (miscellaneous)} (\pm 0.120) \quad R^2 = 0.42^*$$

Equation E3.2

Only cattle rate of biting, cattle total bites per day and sheep grazing time gave significant regressions on the leaf:stem ratio (Table E3.24). The use of the quadratic expression did not improve the fits.

Figure E3.19

The relationship between the C-S difference in diet OMD and sward height



$y = -7.4 + 0.35x\ (\pm 0.143)\ r^2 = 0.33$ *

Table E3.23

The relationships between the cattle and sheep ingestive variates (y) and the bulk densities of the herbage components in the sward and the whole sward (x) where the regressions were significant ($P < 0.05$).

Cattle

OMD	67.3+0.09x (broad-leaved grass) (±0.020)	r^2=0.56**
OMD	73.6-0.48x (miscellaneous) (±0.173)	r^2=0.39*
Intake per bite	0.59 + 0.09 (*Juncus*) (±0.032)	r^2=0.42*
Rate of biting	44.6+0.06x (total green) (±0.026)	r^2=0.30*
Rate of biting	47.6+0.12x (total stem) (±0.053)	r^2=0.29*
Rate of biting	59.4 - 4.30x (*Juncus*) (±1.369)	r^2=0.45**
Total bites per day	35289.1-3533.3x (*Juncus*) (±1059.76)	r^2=0.48**

Sheep

OMD	70.8+0.07x (broad- leaved grass) (±0.020)	r^2=0.48**
Intake per bite	0.87 + 0.13x (*Juncus*) (±0.056)	r^2=0.32*
Grazing time	518.5+0.09x (whole sward) (±0.034)	r^2=0.35*
Grazing time	467.5+0.49x (total green) (±0.218)	r^2=0.30*
Grazing time	515.3+0.91x (fine-leaved grass) (±0.305)	r^2=0.42*
Grazing time	486.8+1.05x (total stem) (±0.429)	r^2=0.33*
Grazing time	533.2 + 0.09x (dead) (±0.039)	r^2=0.32*

Table E3.24

The relationships between the cattle and sheep ingestive variates (y) and the leaf:stem ratio (x), where the regressions were significant.

Cattle

Rate of biting	72.8 - 10.57x (±3.980)	$r^2 = 0.37^*$
Total daily bites	46113.7 - 8549.5x (±3136.59)	$r^2 = 0.38^*$

Sheep

Grazing time	686.6 - 78.83x (±35.219)	$r^2 = 0.29^*$

Discussion

In this section the variations in sward characteristics and ingestive behaviour variates across periods and years are considered first, followed by a discussion of the relationships between the animal and sward variables. Because of the unbalanced distribution of community types within years and seasons, and because of marked changes in some of the swards as a result of deliberate manipulation, the analyses of variance did not include examination of community or seasonal differences. Comments on these aspects of the results are based on examination of the patterns of variation within and between years.

The extent to which animal responses to different swards might be considered to reflect parts of a general pattern of response to changing conditions, and the degree to which the grazing strategies of the cattle and sheep can be regarded as complementary, are dealt with in the General Discussion.

Sward conditions

Newbould (1981) describes the main types of vegetation on rough grazings and their limits to production. As a consequence of the distribution of measurements across communities and years a wide range of sward conditions were covered.

Herbage mass: Differences between the indigenous swards in total herbage mass, total green mass and the proportion of green material in the sward (Table E3.4) reflect differences in previous utilisation and season. The very high herbage mass on both the

Agrostis-Festuca and Nardus swards in 1978 was a result of several years of underutilisation which led to a build-up of dead litter as indicated by the low proportions of green matter.

The imposition of grazing management routines as described in the Methods section resulted in the reduction of the overall herbage mass to levels similar to those found in normal farming practice (HFRO, 1979). The low proportions of green matter in the Agrostis-Festuca and Nardus swards, particularly in the spring of 1979 but also in the Nardus sward in the autumn of both 1978 and 1979 reflect the influence of season. The spring of 1979 was late and herbage growth had only just begun when the measurements were made. The bulk of the accumulated dead material in the Molinia sward was removed by burning in the year prior to the start of the grazing experiments.

The high herbage mass on the Nardus sward compared to the Agrostis-Festuca sward even after two seasons of grazing reflects the greater herbage mass in the Nardus tussocks. The differences between the June and August 1979 and the July and September 1980 measurements on the Molinia sward reflect the deciduous growth form of the dominant species - Molinia caerulea. Growth of the Molinia had only just begun in June 1979 whilst in September 1980 the Molinia was beginning to die off, giving the lower proportion of green matter in the sward in September compared to July (Table E3.4).

The determination of herbage mass on heterogeneous swards requires that the samples be taken at random. Procedures for sampling have been described recently by t'Mannetje (1978) and Frame (1981). In this experiment a modified stratified random sampling procedure was employed, which involved dividing the measurement plots into sub-plots on the basis of topographic, botanical, physical or some other features and then taking samples from each sub-plot in proportion to its area. The herbage mass samples on the *Nardus* sward were further subdivided into tussock, intermediate and intertussock samples to take account of the mosaic of tussock and intertussock vegetation. The results however were presented as mean values for the whole sward. As a consequence the coefficients of variation (CV) were generally larger on the *Nardus* sward than the other swards, ranging from 14.6% to 61.7% with a mean of 46.5%. On the *Agrostis-Festuca* and ryegrass swards the CV's ranged from 18.5% to 24.4% (mean 21.2%) and 22.5% to 23.5% (mean 23.0%) respectively. The CV's for the *Molinia* sward were slightly higher, ranging from 25.5% to 49.2% (mean 35.6%). The range of CV's taken from the literature by Frame (1981) comparing different sampling techniques on sown swards were generally lower than those quoted above (being between 3% and 41%), but the precision of the estimates in the present experiment was reasonable bearing in mind the nature of the vegetation.

The quadrats used on the *Agrostis-Festuca*, *Molinia* and ryegrass swards were rectangular (15 cm x 122 cm) to minimise the effects of small-scale patchiness and were cut to soil level, except the cuts made on the July 1978 *Agrostis-Festuca* sward which were cut to the level of the mat of raw humus which overlay the soil surface. Later the mat layer largely disappeared due to trampling and the increased grazing pressure. On the *Nardus* swards the turves were roughly square to rectangular in shape depending on whether tussock, or intertussock vegetation was being sampled. The herbage was removed down to the mat layer, which remained a constant feature in all samples.

Quadrat cuts were not taken in the drains that crossed the Molinia site. Sampling in the drains would have been extremely difficult, but in retrospect the omission was unfortunate since the majority of the Juncus on the site, which was a regular feature of the diet of the cattle, was confined to the drains.

Sward height: The Agrostis-Festuca and Nardus swards became more uniform in height in 1979 compared with 1978, presumably a result of the overall reduction in herbage mass (Table E3.4). The large increase in sward height between June and August 1979 on the Molinia sward reflects the growth of flower stems in that sward; there was no such difference in 1980 because the flower stems had been produced before the first measurements were made. The small difference in sward height between the May and September 1979 Agrostis-Festuca sward is a result of the grazing between experimental periods, which prevented the growth and maturation of flower stems.

In this experiment sward height was determined from the height of the first hits of the point quadrats. The ryegrass, Nardus, Agrostis-Festuca and Molinia swards had CV ranges and means respectively of 26.0% - 48.5% (mean 37.3%); 39.5% - 69.0% (mean 49.7%); 37.9% - 54.2% (mean 47.4%) and 52.5% - 100.9% (mean 68.6%). These CV's lie in the middle of the range of 11% to 107% quoted by Frame (1981) for sown swards. Variability was greatest in this experiment on the Molinia sward which was the tallest, and on the Agrostis-Festuca and Nardus swards appeared to be greater in the summer than in the autumn. This is not surprising since most of the flower stems had disappeared by the autumn. The derivation of an estimate of sward height from the mean of the "first contact" heights in a series of measurements is likely to underestimate sward surface height relative to procedures in which the highest points of the sward are measured, and sward heights estimated in this way were lower than the maximum height values shown on the figures of density distribution (Appendix figures E3.1.1 to E3.1.14).

Sward structure and botanical composition: The different structures and densities of the sward are illustrated in Appendix Figures E3.1.1 to E3.1.14. Differences between the structures of the swards at comparable times of year were obvious, particularly the differences between the *Molinia* sward and the *Agrostis-Festuca* sward, in July and September, (Appendix figures E3.1.3 & E3.1.13 and E3.1.11 & E3.1.14). There were also differences from measurement period to measurement period on the *Agrostis-Festuca* sward as it was grazed down, though the distribution of components through the sward is also influenced by season (Appendix figures E3.1.3, E3.1.5, E3.1.6 and E3.1.11).

The major difference between the sown ryegrass sward and the indigenous swards was in the distribution of dead material. In the ryegrass sward it was confined almost exclusively to the lower 6 cm of the sward whereas in the indigenous swards it was distributed quite widely through the whole sward. In the most extreme cases of the May 1979 *Agrostis-Festuca* and *Nardus* swards the uppermost horizons consisted almost entirely of dead leaf tips and dead flower stems (Appendix figure E3.1.6 and E3.1.7). To avoid overcomplication of the figures vegetative stem, flower stem and flower head were bulked together. In reality the majority of hits below 6-9 cm were on vegetative stem while those above were on flower stem and flower. Dicots tended to be concentrated in the lower horizons though in the June Nardus and July Agrostis-Festuca swards in 1978 quite large proportions of the dicot Gallium saxatile were found in the upper horizons (Appendix figures E3.1.2 and E3.1.3).

Animal responses.

Diet digestibility and herbage intake: It is apparent from the results and particularly as illustrated by Table E3.6 that the sheep were able to obtain diets of broadly similar digestibility irrespective of sward type or time of year, whereas the OMD of the cattle diet was more variable, being particularly low in the early spring. Furthermore it is apparent that the cattle and sheep differed as to the swards from which they obtained diets of higher or lower digestibility. The reasons for the ability of sheep to obtain diets consistently of higher digestibility than cattle is discussed in detail in the sub-section on diet composition. It is sufficient to say at this stage that the observed OMD of the sheep diets compares favourably with the figures given by Eadie (1967) for sheep grazing Agrostis-Festuca swards. There are no comparable OMD values for cattle diets from similar indigenous swards. The OMD of the diets obtained from the ryegrass swards by both cattle and sheep are similar to values quoted by Hodgson and Jamieson (1981) and Jamieson and Hodgson (1979b). The cattle diet OMD on the indigenous swards are similar to some values reported for cattle on tropical grass swards (Stobbs, 1973b).

Herbage organic matter intake by the sheep on the ryegrass sward in both 1978 and 1979 was rather low in comparison to values published by Hodgson and Milne (1978) for the intakes of sheep grazing similar swards (Table E3.7). HOMILW by the cattle on the ryegrass swards was similar to the values published for non-lactating cattle grazing perennial ryegrass swards (Hodgson and Jamieson, 1981).

In 1978 both cattle and sheep had higher herbage intakes on the indigenous swards than on the ryegrass sward. The reason for this is not clear, but it is unlikely to be due to measurement errors. Estimates of the amount of herbage removed from the ryegrass plot by the animals over the grazing period and the amount of herbage that disappeared between 'In' and 'Out' cuts only differed by 80 kgOM/ha, which can be accounted for by the regrowth of herbage between the time when the animals were removed from the plot and the actual cutting of the 'out' cut two days later (R.D.M. Agnew, personal communication).

The stocking rate was higher on the ryegrass plot than on the other swards which, given the results of Experiment 1 and those of Jamieson and Hodgson (1979b), may have led to a decrease in herbage intake due to limitations in intake per bite (Table E3.8) as a consequence of reductions in sward height and mass.

In 1979, as in 1978, the cattle herbage intakes declined in the autumn relative to the mid-season intakes, irrespective of sward type (Table E3.7). The sheep herbage intakes on the other hand appeared to be more closely related to sward type than to season. Both species had low intakes in the May 1979 <u>Agrostis-Festuca</u> sward, though the sheep figure is in line with those quoted by Eadie (1967).

The digestible organic matter intakes of the cattle varied from 8.6 gDOM/kgLW on the May 1979 <u>Agrostis-Festuca</u> sward to 18.7 gDOM/kgLW on the July 1978 <u>Agrostis-Festuca</u> sward. In the sheep the same two swards also gave the lowest (15.9 gDOM/kgLW) and highest (26.6 gDOM/kgLW) digestible organic matter intakes. The low intakes of digestible organic matter by the cattle on the May 1919 <u>Agrostis-Festuca</u> sward were barely sufficient for maintenance and, if the weather had been more extreme, and particularly if snow had fallen, as is not uncommon at that time of year, then the cattle would have undergone some degree of undernutrition. The sheep digestible organic matter intakes were also relatively low but, whilst adequate for mature, barren animals, would have been insufficient to meet the nutrient requirements of lactating animals (ARC, 1980).

Differences between 1978 and 1979 in the levels of intake by both the cattle and sheep may be due to differences in the structure and botanical composition of the swards, but may also be due to differences in the live weights of the animals. Langlands (1968) found that sheep that had undergone a period of undernutrition had higher intakes than sheep that had not been restricted, though the difference in mean live weight was small. Arnold and Birrel (1977) found that intakes of herbage were higher in animals that were lighter due to a period of undernutrition. Hodgson, Peart, Russel, Whitelaw and MacDonald (1980) found slight increases in herbage organic matter intakes (HOMI) in lactating cows that had previously been on low planes of nutrition. In that experiment the difference in mean live weight at turnout was only 10 kg. In the present experiment no live weight is available for the non-fistulated cattle at the start of grazing in 1979 (Table E3.5) but, given the low absolute intakes on the Agrostis-Festuca sward in May of 1979, it seems unlikely that they would have gained more than 10 to 20 kg in live weight between the beginning of the grazing season and the end of the Nardus measurement period. On this basis, live weights of the non-fistulated cattle would have been about 100 kg higher in 1979 than in 1978. In these mature animals variations in body weight would be attributable largely to differences in body reserves.

The low live weights of the cattle in 1978 relative to those of 1979 (Table E3.5) might well account for the higher overall intakes observed in 1978, as a result of a higher intake drive rather than a lower live-weight adjustment. The live-weight differences were relatively much less in the sheep and differences in herbage intake by the sheep are more likely to have been a result of differences in sward structure than differences in live-weight. Within-years differences in sward structure are likely to have been important in determining the level of herbage intake in the cattle, particularly regarding differences between intakes on the short Agrostis-Festuca sward in May 1979 and other swards later in the year (Table E3.7). The influence of sward structure and botanical composition on intake are discussed in a later section.

The OMD of the diet was predicted from in-vitro digestion of extrusa samples with reference standards obtained from in-vivo estimation of herbage collected from similar plant communities and fed frozen to sheep at a level close to appetite (Armstrong and Common, 1981). The use of standards prepared from herbages fed frozen at slightly below appetite avoided some of the problems associated with standard procedures where dried forages are fed at maintenance levels, and there was the added advantage that the reference standards closely approximated the range of herbages that were grazed.

Oesophageal fistulated animals have been widely used to obtain material from which in-vitro OMD is determined. The OMD is then generally used, in conjunction with estimates of faecal output from non-fistulated animals, in the calculation of herbage intake. It is important therefore that the diets of the two groups of animals are similar. Appendix 5 gives the details of a comparison of the diets of a comparison of the diets of fistulated and non-fistulated cattle and sheep in which it was found that the diets of the two groups did not differ significantly in their botanical composition.

Hodgson and Rodriguez (1970) discussed the potential sources of error involved in the estimation of herbage intake and suggested that, although OMD estimated by the in-vitro technique could be used with some confidence in the calculation of herbage intake, some caution was necessary particularly when diets of high digestibility were involved.

The coefficients of variation for the determination of herbage intake in this experiment ranged from 8.0% to 11.5%, which compares well with the range given by Jamieson (1975) of 6.2% to 21.5%, and by Hodgson and Rodriguez (1970) of 5% to 13%.

Intake per bite: The intakes per bite by the cattle calculated from HOMILW and total daily bites (Table E3.8) were very much lower on all swards, particularly in 1979, than the figures given by Hodgson and Jamieson (1981) for lactating cows grazing ryegrass swards, and were generally lower than the figures for calves grazing ryegrass swards (Jamieson and Hodgson, 1979b). The intakes per bite by the sheep calculated from HOMILW and total daily bites were somewhat larger, however than the values given by Jamieson and Hodgson (1979b) for lambs. In contrast, the use of the alternative technique in which weight per bite is calculated from the weight of extrusa collected divided by the number of bites taken and expressed as a DM/bite gave low values for the sheep compared to those found by Allden and Whittaker (1970) for grazing sheep (Table E3.25). Table E3.25 compares the weights per bite by the cattle in 1979 calculated from the weight of extrusa with values obtained by the same method by other workers on both temperate and tropical swards.

Table E3.25

The ranges of intakes per bite (gOM/bite) calculated from the weight of extrusa collected from both cattle and sheep in 1979 compared with other published results.

	Cattle	Sheep
Present study	0.20 - 0.96	0.036 - 0.110 (0.042 - 0.124 gDM/bite)
Allden and Whittaker (1970)	-	0.025 - 0.420 gDM/bite
Stobbs (1973a)	0.13 - 0.52	-
Chacon and Stobbs (1976)	0.07 - 0.28	-
Jamieson and Hodgson (1979a)+	0.015 - 0.445	-
Jamieson and Hodgson (1979b)+	0.082 - 0.290	-
Hendricksen and Minson (1980)	0.090 - 0.410	-
Hodgson and Jamieson (1981)++	0.604 - 1.565	-

+ = calves. ++ = lactating cows.

It would appear that on the indigenous swards the cattle and sheep had intakes per bite that were generally lower than have been found on temperate sown swards but, in the cattle at least, intakes per bite were higher on the indigenous swards than on tropical swards.

The measurement of weight per bite by recording the number of bites taken during the collection of extrusa samples depended on the co-operation of the animals. In 1978 the sheep frequently refused to graze with throat plugs and so little data was collected by this method. However, after a winter experiment involving the use of throat plugs the animals were much more tolerant in 1979, thus enabling a satisfactory collection of extrusa samples in that year. The high CV reflects the variation in intake per bite between the swards. Though estimates of rate of biting and grazing time estimates are considered to be representative, intakes per bite calculated from HOMILW divided by total daily bites were lower on all but one occasion than the weights per bite obtained from the weight of extrusa collected divided by number of bites taken in the collection of the extrusa (Table E3.10). Jamieson and Hodgson (1979b) attributed a similar difference to a combination of overestimation of rate of biting and overestimation of mean bite size from extrusa records. In this experiment the greatest differences between the two methods were in the cattle intakes per bite on the Molinia and ryegrass swards. As described later, cattle grazing time on the June Molinia sward was felt to be overestimated to some degree. On this sward, too, some difficulty was encountered in ensuring that all bites were counted during extrusa collection. Errors of this sort would account for the observed differences in the July ryegrass and August Molinia measurements.

The coefficient of variation for intakes per bite derived from HOMILW and total daily bites ranged from 9.3% to 15.0%, whilst the CV for weights per bite derived from the weight of extrusa collected and the number of bites taken was very high at 47.8%. This latter figure may be compared with those of Jamieson (1975), using the same technique but on sown swards, where the CV ranged from 18.4% to 29.1%.

Though the estimation of the weight of herbage taken per bite may be more accurate when counting the number of bites taken to collect a given weight of herbage than the estimation of intake per bite obtained by dividing daily herbage intake by total daily bites, the technique is of limited use if the animals will not perform consistently. For this reason, intake per bite obtained by dividing daily herbage intake by total daily bites is the preferred method.

Rate of biting: The mean daily rates of biting varied markedly from sward to sward (Table E3.11), with a seasonal effect being significant in both 1978 and 1979 ($P < 0.001$). In 1978 rates of biting were not significantly different on the *Agrostis-Festuca* swards but increased on the *Nardus* swards in the autumn. In 1979 rates of biting were again not different on the *Agrostis-Festuca* swards but, while the sheep rates of biting did not change significantly on the *Nardus* and *Molinia* swards, the cattle rates of biting decreased on both swards over the year.

Changes in rates of biting between swards and within swards over season are almost certainly due to changes in the botanical composition and structure of the swards. Most previous studies have examined changes in rate of biting in relation to sward structure on temperate, sown swards (Allden and Whittaker, 1970; Hodgson and Milne, 1978; Jamieson and Hodgson, 1979 a & b; Hodgson, 1981; Hodgson and Jamieson, 1981), though some work has been carried out on tropical swards with cattle (Stobbs, 1974). The influence of the structure of the swards on rate of biting is discussed later.

The 20-bite method of estimating rate of biting as used by Jamieson (1975) and Jamieson and Hodgson (1979a) is a measure of the potential rate of biting but, as described in Experiment 1, the technique was modified somewhat to allow for longer periods between bites or groups of bites during which time the animals were actively selecting or manipulating herbage. Thus the records collected are less likely to be overestimates than those of Jamieson (1975). CV's for rates of biting varied from 9.4% to 13.1% in comparison to those given by Jamieson (1975) which ranged from 3.9% to 10.2%. Diurnal variation in rates of biting were shown to be important (Table E3.12) and thus measurements should be made during at least the major grazing periods of the day to avoid the risk of over- or under-estimating the mean daily rate of biting. In this experiment the majority of records were taken during the first major grazing period after dawn and in the late afternoon and evening. Examination of Figures E3.2 to E3.6 suggests that the mean of measurements made early and late in the day should provide a reasonable estimate of the mean daily rate of biting. Other evidence for diurnal changes in rate of biting are conflicting. Elizabeth MacPherson (personal communication) found that sheep grazing ryegrass swards had lower rates of biting in the middle of the day than in either the morning or the evening, but Jamieson and Hodgson (1979a), working with calves, observed no difference in rate of biting between grazing periods. There is some evidence that rate of biting declines with time spent grazing within individual grazing periods (Hancock, 1950; Stobbs, 1974) but this aspect of variation was not investigated.

Grazing time: The observed mean grazing times lie within the published ranges of grazing times from 265 min/day (Hancock, 1954) to 816 min/day (Stobbs, 1970) for cattle and from 420 min/day (Arnold, 1960b) to 700 min/day (Allden and Whittaker, 1970) for sheep. As with rate of biting, grazing time is believed to be modified by the animals in response to changes in sward conditions. In 1978 in particular, grazing time increased later in the year in conjunction with increases in rates of biting. Both increases were in response to a reduction in intake per bite. It would appear from Table E3.13 that the cattle were more consistent in their grazing times than the sheep. The reasons for this and its consequences are discussed in a later section.

The use of vibracorders enabled large amounts of data on grazing time to be collected. In 1978 there were some problems related to the waterproofing of the equipment, but this was largely overcome by the use of rings cut from tyre inner tubes and stretched around the instruments, covering the slight gap between the back and front plates. This problem may be reflected in the CV of estimates of grazing time which were 11.1%, 7.7% and 8.1% respectively for 1978, 1979 and 1980. Jamieson and Hodgson (1979b) found that manual records of grazing time made on one day per week were 7% lower than the weekly mean grazing time obtained from vibracorders and, though Jamieson (1975) suggested that grazing time measured by vibracorders could be overestimated in circumstances where the chart traces were not particularly clear, Jamieson and Hodgson (1979b) suggested that the presence of observers probably interfered with grazing activity to a degree. In general, in this experiment, records were reasonably clear and interpretation was not difficult, though unclear records tended to be more common on the sheep than the cattle.

Grazing time did not appear to be greatly affected by day to day variations in the weather though on the June 1979 Molinia sward it appeared that the animals, particularly the cattle, were on some days badly troubled by flies. Extremely high readings (over 1000 min/day) were therefore omitted from the analysis.

Most of the differences between the cattle and sheep in their ingestive behaviour were consistent across swards or else the variability could not be explained by the principal components used. The difference between the grazing times of the cattle and sheep was explained by the principal component 'low sward quality' (Figure E3.14). As sward quality declined so the sheep grazed for longer than the cattle. This response may reflect an inability of the sheep to increase rate of biting as selectivity increases.

The composition of the diet

During analysis of the extrusa samples, grass vegetative stem as such was rarely observed, but instead this fraction appeared as sheath-like material. It was found impossible to separately identify sheath material from flower stem and from vegetative stem and so all stems and sheaths were bulked together with flower heads into a total stem category. In order that proper comparisons could be made, particularly when it came to carrying out principal component and regression analysis, vegetative stem was bulked with flower stem and flower head in the sward samples. This was not an ideal solution in that grass flower stems and heads are concentrated in the upper horizons of the sward whilst vegetative stems are found almost exclusively in the lower horizons. As a consequence there is the possibility of different individual animals or even different animal species having diets containing similar proportions of total stem, but which are in fact composed entirely of vegetative stem on the one hand and flower stem on the other, leading to misinterpretation of the results. Appendix Table E3.17 shows the composition of total stem in the cattle and sheep diets.

With the single exception of the June 1978 Nardus sward the cattle diets always contained a significantly lower proportion of total green material than sheep diets when the proportion of total green in the sward was 0.50 or less (Tables E3.4 and E3.14.1). The lack of a significant difference between the cattle and the sheep on the June 1978 Nardus sward was probably due to the large proportions of green grass flower stem and flower eaten by the cattle. However Tables E3.17.1 to E3.17.3 show that both cattle and sheep were able to concentrate green material in their diet even though the proportion of green material in the sward was less than 0.50.

Few significant differences were found in the proportions of grass leaf in the diets of cattle and sheep, though generally the cattle ate smaller proportions than did the sheep, a finding in agreement with that of Van Dyne and Heady (1965). Other studies on the diet composition of cattle and sheep by Cook, Harris and Young (1967), Dudzinski and Arnold (1973) and Wilson (1980) did not distinguish between separate grass fractions. When grass leaf and total grass stem was bulked it was found that cattle ate more grass than sheep on only 7 of the 14 swards, in contrast with the findings of Cook et al (1967) who found that cattle consistently ate more grass than sheep; however Wilson (1980) found that cattle consistently ate less grass than sheep, whilst Dudzinski and Arnold (1973) found that cattle consumed less grass than sheep on 14 out of 17 trials.

The larger proportion of grass stem (principally flower stem and head) in the cattle diet relative to the sheep is consistent with the findings of Van Dyne and Heady (1965) though it must be noted that on the May Agrostis-Festuca and May Nardus swards in 1979, prior to the main production of flower stem, the cattle had lower proportions of total stem in their diets than the sheep, due mainly to the relatively large proportions of sheath in the sheep diet (Appendix Table E3.17). Taking into account the season it is likely that the majority of this sheath material came from vegetative rather than flower stems. The significance of this is discussed later in relation to the structure of the sward and the horizon in the sward in which the animals grazed. The lower proportions of dicots in the cattle diet relative to the sheep is also consistent with the findings of Van Dyne and Heady (1965) and Dudzinski and Arnold (1973).

Where the number of variates used to describe a sward is very large and, as is frequently the case, where the variates are inter-correlated, the use of multiple regressions is at best unsatisfactory. In these circumstances it is considered more satisfactory to use a technique such as principal component analysis that not only reduces the number of variates but transforms the variates to new variables that are linear combinations of the original variates (Dudzinski, 1975). Dudzinski and Arnold (1973) and Langlands and Sanson (1976) used principal component analysis to examine the differences in diet composition of cattle and sheep grazing together, on sown swards in Australia. In this experiment principal component analysis was used to reduce not only the variates describing the composition of the sward but those describing the composition of the extrusa of the cattle and sheep.

The use of principal component analysis indicates that the cattle diet could be described in terms of its leafiness and stemmness as well as its quality. The sheep diet on the other hand could be described in terms of quality and selection for components (Table E3.19.1). The changes in the proportions of herbage components in the diets of cattle and sheep in response to variations in the principal components 'low sward quality' and 'opportunity for selection' were similar (Tables E3.20.5 and E3.20.6).

Table E3.21.2 indicates that the differences between the diets of cattle and sheep in the proportions of broad-leaved grass, total grass stem, dicots, miscellaneous spp and Juncus do not change significantly across swards. This may reflect a consistent difference across swards (i.e. cattle always eat more grass stem and less dicots etc. than the sheep) or a highly variable response indicating that diet composition was unrelated to the sward variates used to derive the principal components. The evidence suggests that the former was the case, the reasons for the consistency of the difference between the diets of the cattle and sheep, total grass stem and dicots in particular being illustrated by examination of Appendix Figures E3.1.1 to E3.1.14 which show the vertical distribution of the major components within the sward canopy, and Table E3.16 which shows that the cattle spent proportionally more time grazing the upper sward horizons than did the sheep. Since grass flower stem and flowers were concentrated in the upper and dicots in the lower horizons, by concentrating their grazing in the upper horizons, the cattle were likely to consume more stem and less dicots than the sheep. However there is the question of whether the horizon in which grazing takes place determines the diet or whether diet selection determines the horizon in which grazing takes place. The selection ratios (Tables E3.17.1 to E3.17.3) suggest that cattle are highly selective for grass stems at those times of year when the flower heads are emerging, but avoid grass stems at other times of the year. Similarly, sheep have higher selection ratios for dicots than do the cattle on all swards. However, it would appear that sheep, by virtue of their narrower muzzle and more mobile upper lip, can have a greater discriminating ability than cattle and are able to penetrate deeper into the sward and select out components that cattle cannot reach.

It may well be that cattle consume large quantities of stem because the combination of sward structure and their method of grazing does not permit them to do otherwise. _Juncus,_ unlike grass flower stem and flower, tends to be distributed evenly (vertically) through the sward. If the suggestion is correct that sheep do not often graze plants from the bottom upwards, in the sense of biting off leaves or stems near their bases (Arnold, 1964), then this could explain the low proportion of Juncus in the sheep diet because the sheep were grazing around the base of the Juncus plants.

The evidence from the measurements of the length of leaf grazed (Figure E3.7) suggests that the sheep did graze from the surface of the leaf stratum downwards rather than biting the leaves off at their bases.

Figure E.15 shows that as the quality of the sward declined the difference between the proportions of total green herbage in the diets of cattle and sheep increased. This figure also indicates that on the Molinia and ryegrass swards the proportions of total green material in cattle diets were equal to or higher than these in sheep diets. Dudzinski and Arnold (1973) obtained a similar result. By grazing towards the base of the sward the sheep graze in horizons containing higher proportions of dead material and so, even though they are generally more selective than cattle, ingest diets somewhat lower in the proportion of total green material. On shorter swards the cattle, being less selective, cannot avoid the dead material. The same conclusion can be drawn from the relationships between the difference between cattle and sheep in diet OMD and sward height (Figure E3.19).

The differences between the cattle and sheep in the proportions of total grass leaf and fine-leaved grass in the diet, when related to the principal component 'opportunity for selection', suggest that in certain circumstances the cattle can be as selective as the sheep. Arnold and Dudzinski (1973) found that though the proportion of stem in the cattle diet was always higher than in the sheep diet the difference increased with increasing 'total bulk' of the swards. No such relationship was found in this experiment, apparently because the cattle concentrated their grazing on flower stems and flowers on the June 1978 Nardus sward, the July 1978 Agrostis-Festuca sward and the August 1979 Molinia sward (Table E3.14.5) whilst the sheep selected relatively large proportions of dicots on the same swards (Table E3.14.5).

Surprisingly perhaps, the differences in the botanical composition of the diets of the cattle and sheep did not result in large differences in diet OMD. The proportions of total green, broad-leaved grass and total stem were all significantly correlated with the OMD of the cattle and sheep diets (Appendix 4) with the largest differences in diet OMD occurring on the Agrostis-Festuca and Nardus swards in the spring and autumn of 1979; in both seasons the cattle had markedly lower proportions of total green material in their diets than did the sheep, substantially so in the spring.

Sward structure and ingestive behaviour: The structure of swards, both temperate and tropical, has been shown to influence the herbage intake of grazing animals by limiting intake per bite and rate of biting (Arnold and Dudzinski, 1967; Allden and Whittaker, 1970; Stobbs, 1973 a & b, 1975; Stobbs and Hutton, 1974; Chacon and Stobbs, 1976; Hodgson, 1977, 1978; Hodgson, Rodriguez Capriles and Fenlon, 1977; Chacon, Stobbs and Dale, 1978; Hodgson and Milne, 1978; Jamieson and Hodgson, 1979 a & b; Hodgson and Jamieson, 1981). However all the above studies were carried out on sown swards with relatively more uniform structures and botanical composition than the swards studied in this experiment.

The structure of a sward is a function of its mass, its height, its botanical and morphological composition and the distribution of components through the canopy. Under the circumstances of this experiment herbage mass had no significant influence on intake, intake per bite, rate of biting or grazing time. This is in contrast with the findings of Allden and Whittaker (1970), Stobbs (1973b), Chacon and Stobbs (1976), Hodgson and Milne (1978) and Jamieson and Hodgson (1979b). However, Allden and Whittaker (1970), Stobbs (1973 a & b) and Hodgson (1981) have all suggested that herbage mass has a smaller influence on ingestive behaviour than other sward characteristics, such as height and leaf density at the sward surface.

It is generally agreed that intake per bite is the major determinant of daily herbage intake and that rate of biting and grazing time change to a greater or lesser degree to compensate for reductions in intake per bite (Chacon and Stobbs, 1976; Chacon, Stobbs and Dale, 1978; Hodgson and Milne, 1978; Hodgson, 1981). In this experiment intake per bite in both cattle and sheep was found to increase linearly with increasing sward height (Table E3.22, Figure E3.18). The tendency for intake per bite to decline slightly on the tallest swards was not significant. It is possible that sward height was underestimated on the taller swards relative to the shorter swards due to the difficulties of recording 'hits' with the point quadrat on very tall swards. This would have the effect of increasing the curvilinearity of the response, particularly in the case of the cattle. Stobbs (1973 a & b), working with cattle on tropical swards, found a negative relationship between intake per bite and sward height and suggested

(Stobbs, 1975) that the decrease in intake per bite with increasing sward height was due to a decline in the density of the sward in the upper horizons which made prehension of herbage difficult. In this experiment the density of herbage in the upper 6 cm of the swards varied from 39 kgDM/ha/cm on the October 1978 Nardus sward to 0.3 kgDM/ha/cm on the July 1980 Molinia sward. These values were estimated from the number of hits in the surface horizons as proportions of the total herbage mass and are low in relation to the values given by Stobbs (1973b, 1975) 5-440 kgDM/ha/cm and Hodgson (1981) 34-247 kgOM/ha/cm, though the values given by Stobbs are for the top 15 cm of the sward. These low surface density values certainly help to explain the difference in bite size found between the cattle and sheep, particularly since the sheep tended to graze deeper in the sward than the cattle. However the surface conditions cannot have restricted intake per bite to any great extent otherwise the positive response of intake per bite to increasing sward height would not have occurred. Intake per bite did not alter significantly with changes in the density of the sward. Though both cattle and sheep did show a positive response in intake per bite to increasing Juncus density (Table E3.23) the result is of limited biological significance since the sheep ate practically no Juncus (Table E3.14.7).

The positive relationship between intake per bite and sward height in the cattle and sheep was matched by a negative relationship between rate of biting and sward height (Table E3.22 and Figure E3.18). Similar relationships, where increasing rate of biting compensates for declining intakes per bite as sward height is reduced, have been described by Chacon and Stobbs (1976) and Chacon, Stobbs and Dale (1978) working with cattle on tropical swards, and by Allden and Whittaker (1970) working with sheep on ryegrass swards. Hodgson (1981), working with calves and lambs, reported a similar response under continuous grazing management but not under strip-grazing management. No such relationship was found in Experiment 1 with the cattle, though the sheep did increase rate of biting to compensate for a reduced intake per bite on one of the two swards. In Experiment 1 the lack of the normal compensatory effect was due, it is suggested, to the animals reducing their intakes as a consequence of the very high intakes on the first few days after entry to a new paddock.

As with intake per bite the cattle and sheep rates of biting showed some evidence of curvilinearity of response to increasing sward height, though again the improvement of the fit of the regression due to the use of the quadratic expression was not significant. In the cattle rate of biting was positively correlated with the density of some of the sward components (Table E3.23); the sheep, however, increased grazing time rather than rate of biting in response to an increase in sward density. Also, the cattle responded to an increasing leaf:stem ratio by reducing their rate of biting, whilst the sheep responded by reducing grazing time (Table E3.24).

It is perhaps surprising that the cattle should reduce their rate of biting as the leaf:stem ratio increased, while increasing rate of biting in response to the density of total green material and total stem. This apparent conflict of results can be explained in relation to the structure of the swards and the composition of the total stem component. The lower rates of biting on the swards with the highest leaf:stem ratios, notably the Molinia swards, was most probably due to the observed increase in intake per bite

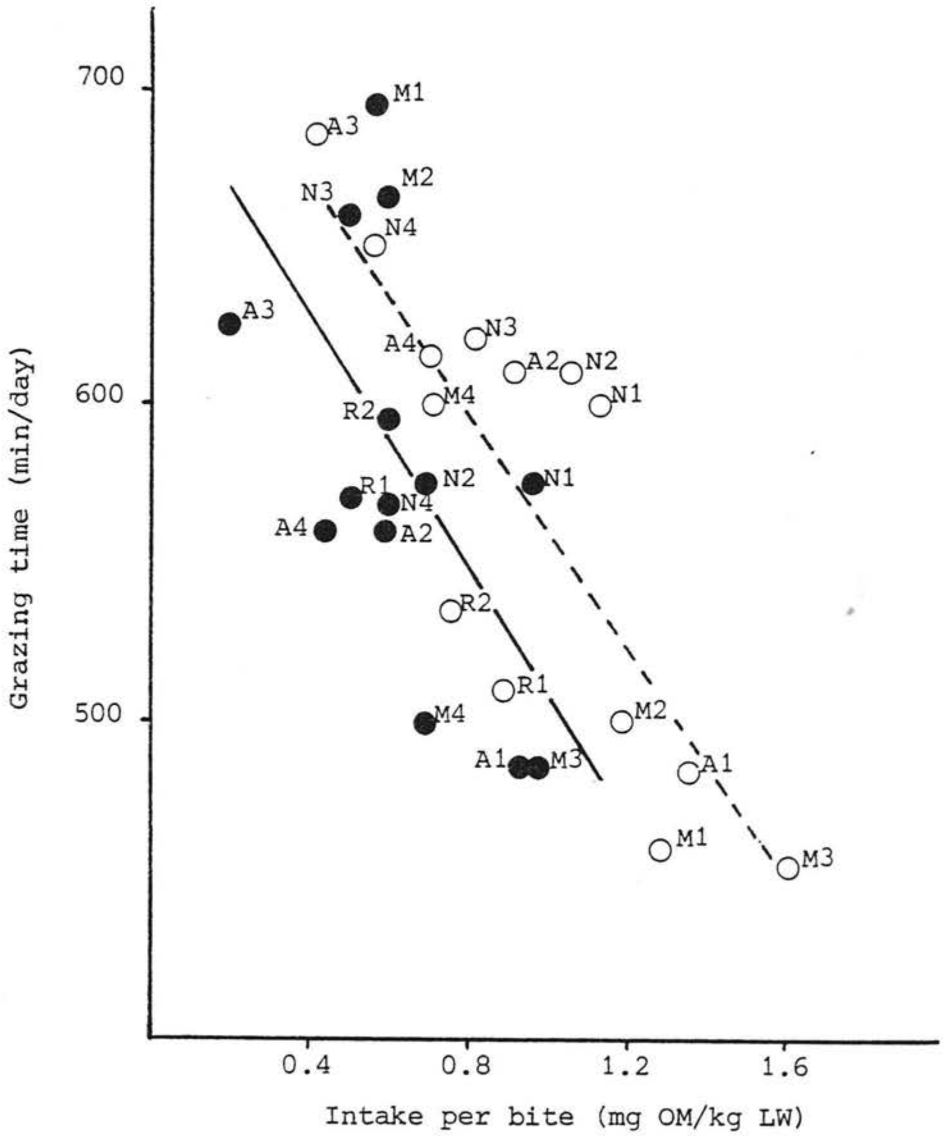
(Tables E3.8 and E3.9). The structure of the *Molinia* tussock, with its dense mass of erect leaves, enables large bites to be taken, if the animals inserted their heads through the upper flower head and flower stem horizons. The other major dietary component for the cattle on the *Molinia* swards was *Juncus* which also grew in dense masses and allowed the prehension of large bites. However it was observed that animals grazing both sward compnents frequently had material hanging outside their mouths which was drawn in and chewed before the next mouthful was taken, thus tending to reduce the rate of biting. The increase in rate of biting by the cattle with the increase in the density of total stem in the sward can be readily explained by the fact that the stem component of the densest swards was largely vegetative stem, which, as it occurred at the base of the sward, was seldom grazed by the cattle and so had little influence on rate of biting, but rather, by raising the level of the leaf horizon, increased the accessibility of the leaf.

The sheep increased grazing time rather than rate of biting in response to increasing stem density. This response suggests that the animals were compensating for a decreased intake per bite, but were unable to increase rate of biting due to the greater selectivity that was required as a result of the increase in stem. Chambers *et al* (1981) suggested that the increase in the ratio of manipulative jaw movements to bites reduced rate of biting. This was in response to increases in sward height, but is also likely to occur when animals become more selective. As the leaf:stem ratio increased intakes per bite increased, but the animals responded by decreasing grazing time rather than rate of biting.

Rate of intake, calculated from intake per bite and rate of biting, increased linearly and significantly with increasing sward

Figure E3.20

The relationship between grazing time and intake per bite in the cattle and sheep



● = Cattle ——— $y = 704.8 - 190.4x$ (±74.83) $r^2 = 0.35$ *

○ = Sheep - - - - - $y = 739.4 - 179.8x$ (±40.74) $r^2 = 0.62$ ***

height in the cattle. This was not the case in the sheep, in which variations in intake per bite and rate of biting tended to cancel one another out (Table E3.22 and Figure E3.18). Allden and Whittaker (1970) found an asymptotic relationship between rate of intake and sward heights whilst Hodgson (1981) found a significant linear relationship. Both Allden and Whittaker (1970) and Hodgson (1981) worked with sheep grazing sown ryegrass swards with relatively little opportunity for selection by the animals, and where the grazed horizon occurred at the sward surface. In the present experiment the sheep generally did not graze the surface horizons, particularly on the taller swards, but in contrast grazed in the leaf horizons some way below the sward surface, and thus rate of intake was largely independent of the actual sward surface characteristics. By increasing rate of biting when intake per bite declined the cattle were able to maintain a more constant rate of intake than the sheep.

As intake per bite increased so the time spent grazing decreased (Figure E3.20). This compensatory response has been observed in sheep and calves and lambs grazing sown temperate swards (Allden and Whittaker, 1970 Jamieson and Hodgson, 1979b) and in cattle grazing tropical swards (Stobbs, 1970). There is evidence (Allden and Whittaker, 1970; Chacon and Stobbs, 1976; Chacon, Stobbs and Dale, 1978; Jamieson and Hodgson, 1979b; Hendricksen and Minson, 1980), to suggest that under certain sward conditions animals are unable to fully compensate for reduced intakes per bite by increasing grazing time and in consequence herbage intake declines. Stobbs (1973) has suggested that cattle grazing tropical swards seldom took more than 36,000 bites per day and that intakes per bite would have to be 0.3 gOM or greater if herbage intake was not to be limited. This figure of 0.3g OM is equivalent to 0.75 mg OM/kgLW and it is clear from Table E3.8 that intake per bite in the cattle was often well below that figure, particularly in the spring of 1979. However the total daily bites by the cattle ranged from 27,100 bites per day on the June 1978 Nardus sward to 45,600 bites per day on the May 1979 Agrostis-Festuca sward. The total daily bites by the sheep ranged from 20,300 on the June 1979 Molinia sward to 48,800 on the May 1979 Agrostis-Festuca sward. The maximum values are greatly in excess of the maximum values recorded by Jamieson and Hodgson (1979b) for calves (36,700) and lambs (33,200), taking into account the differences between the methods of estimating rate of biting.

The low intakes per bite by both species on the May 1979 Agrostis-Festuca sward relative to their intakes on the other swards may be a result of the combination of the high proportion of dead herbage in the sward and the low sward height, (Appendix Figure E3.1.6). Barthram (1980) showed that sheep confine their grazing to a layer above the sward horizon containing the bulk of the vegetative stem and dead material, and he suggested that sheep are unwilling to graze into this horizon even where the result is a reduction in herbage intake. It is not unreasonable to expect that bite depth and hence intake per bite will decline in cattle, as in sheep, as the animals graze down into the horizons containing increasingly greater proportions of dead material. The results of the detailed measurements show that the length of leaf removed by both the cattle and sheep declined with decreasing leaf length, but that over the range of leaf lengths found in this experiment the response by both animal species was linear with no evidence of a cut-off point either at the top or bottom of the range of leaf lengths (Figure E3.7).

Since the width of the mouth is limited animals can only increase intake per bite by either compressing a larger volume of herbage into the same spece or by increasing the length of leaf removed at a bite (i.e. increasing the depth of the grazed horizon). The short grazing periods used, and observations on the animals whilst they grazed suggested that the herbage removed from grazed patches was the result of single rather than multiple bites. Though this cannot be shown to be absolutely true the assumption is made that the amount of herbage removed represents the amount taken at a single bite and thus the result indicated in Figure E3.7 is that animals are able to increase their intakes per bite by increasing the length of leaf ingested.

The results of this study suggest that the ingestive behaviour responses of the cattle and sheep to a wide range of sward conditions essentially follow the same pattern as that shown by animals grazing temperate sown swards, namely an increase in intake per bite with increasing sward height together with a decrease in rate of biting and grazing time (Allden and Whittaker, 1970; Jamieson, 1975; Jamieson and Hodgson, 1979 a & b; Hodgson, 1981). There was, however, a suggestion that the responses in intake per bite and rate of biting to increasing sward height might have been curvilinear, particularly where the increase in sward height led to a decrease in sward density. Further experimentation on taller swards might reveal whether this was the case. If so, then the response of the cattle and sheep to the tallest swards resembles that described by Stobbs (1973 a & b, 1975), Chacon and Stobbs (1976), and Chacon, Stobbs and Dale (1978) for cattle grazing tall, tropical swards with low surface densities, where intake per bite decreased with increasing sward height. This lends weight to the suggestion (Hodgson, 1981) that the apparent conflict between responses measured on temperate and tropical swards may simply reflect the fact that observations have been made at opposite ends of a response curve.

The results from Experiment 1 suggest that under certain circumstances animals can have very high herbage intakes over short periods of time. In these circumstances herbage intake appears to be controlled by the volume of herbage taken per bite, since intake per bite declined very rapidly with no commensurate increase in rate of biting or grazing time. Since herbage mass and sward height were above those limits postulated by Jamieson (1975) of 1000-1200 kg DM/ha and 7.5 cm below which herbage intake might be limited, it would appear that the observed decline in intake per bite and hence herbage intake was being influenced not by sward parameters but by internal controls.

In Experiment 3 the cattle were less variable than the sheep in their intakes per bite, rates of biting and grazing times across periods, indicating that they did not modify their responses to changes in sward conditions as readily as the sheep. The sheep had less variable diet OMD's than the cattle indicating that they selected a more consistent diet. The sheep had higher intakes per bite (mg OM/kg LW) and slower rates of biting, whilst grazing time was not consistently longer or shorter than in the cattle. Since the sheep had, on a live-weight basis, higher daily intakes it can be concluded that intake per bite had the greatest influence in determining daily intake. This result is in line with the results of Hodgson and Milne (1978), Jamieson and Hodgson (1979b) and Hodgson (1981).

General Discussion

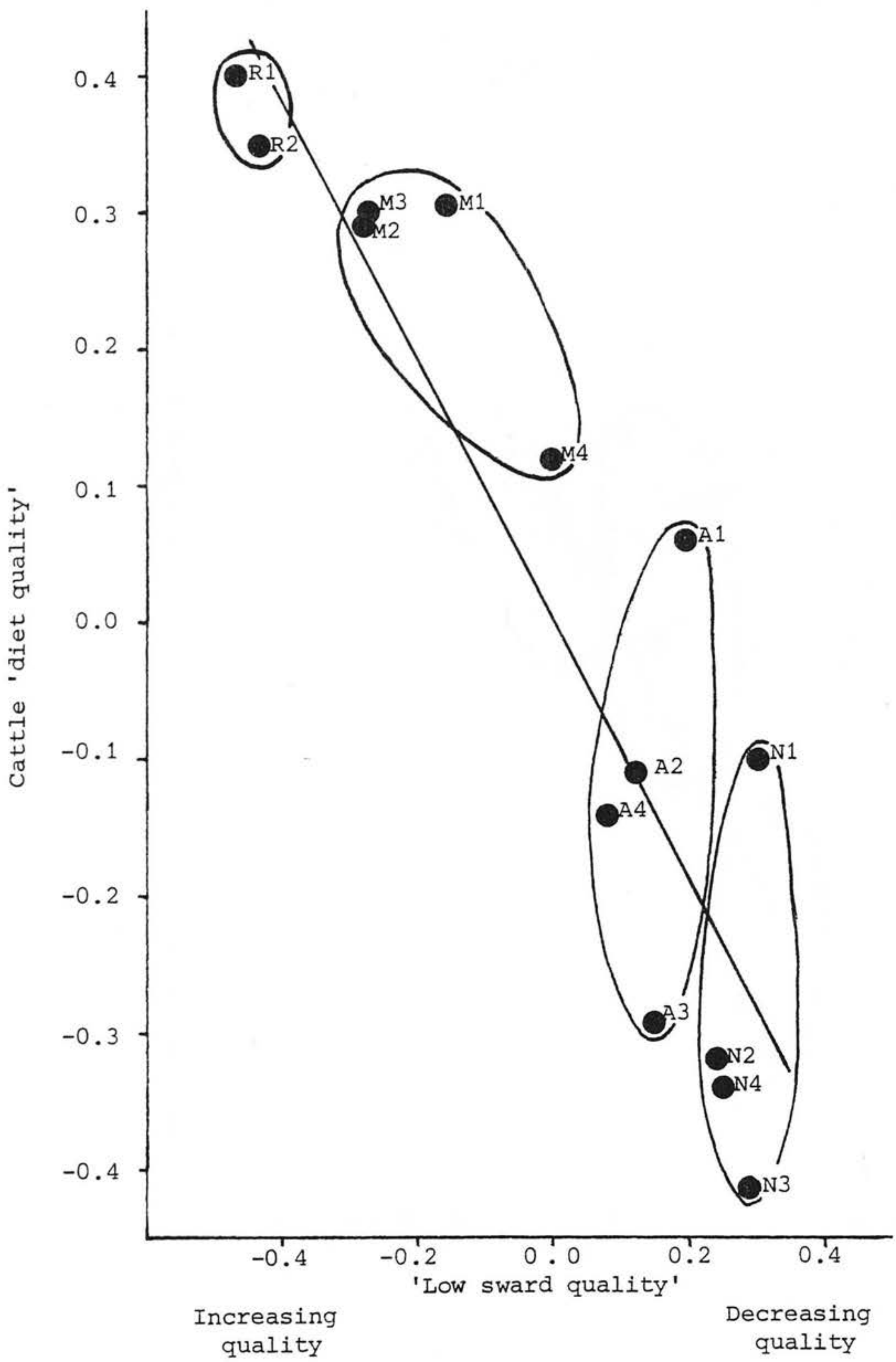
The position regarding the responses of the cattle and sheep to the swards as communities is not unequivocal in that many of the responses, particularly those relating ingestive behaviour to sward variates derived by principal component analysis, indicate that the responses are to individual swards rather than to characteristics common to all the swards. However, Tables E3.20.1, E3.20.2, E3.20.5, E3.20.6, E3.22, E3.23 and E3.24 indicate that a number of the animal variates show responses to certain sward parameters that are consistent across swards. For example, in both cattle and sheep intake per bite and rate of biting respond to decreasing sward height irrespective of the vegetation type, and this applies to other animal variates regressed on sward density and leaf:stem ratio (Tables E3.22, E3.23 and E3.24). These particular sward variates reflect management and season effects, however, and thus do not fully reflect characteristics specific to each community.

The principal component 'low sward quality' describes a characteristic which separates the swards into the separate communities. Figures E3.21 and E3.22 illustrate this point and show the relationships between cattle and sheep 'diet quality' and 'low sward quality'. The figures are presented separately since the eigenvectors in the principal component 'diet quality' have different weightings in the cattle and sheep. Even though the swards have values for 'low sward quality' that do not overlap, the relationships appear to be consistent across the range of swards, implying that the differences between the swards are differences in degree rather than kind.

A resolution of the question of whether the animals are

Figure E3.21

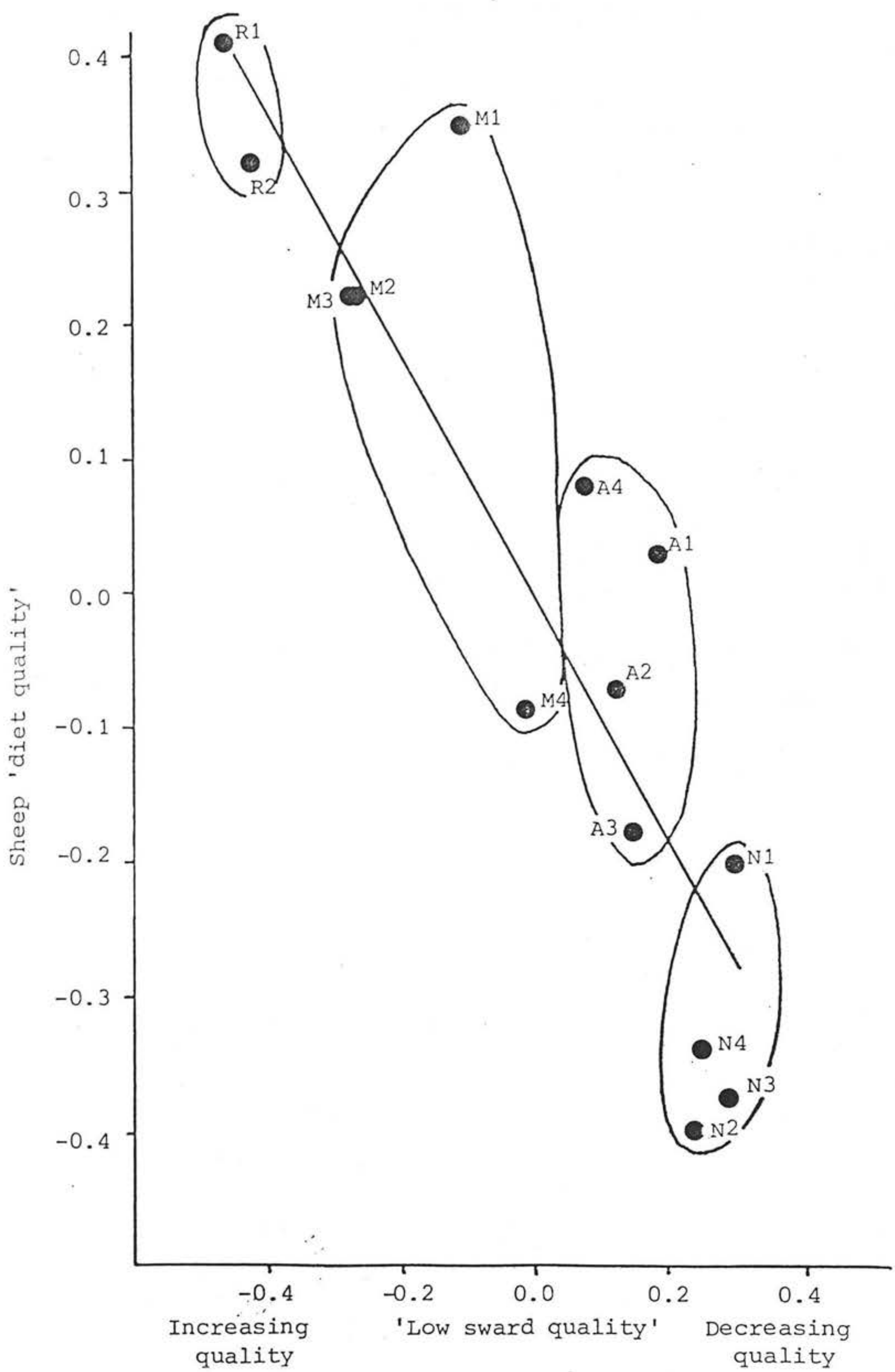
The relationship between cattle 'diet quality' derived from the proportions of herbage components in the cattle diet, and 'low sward quality' derived from the proportions of herbage components in the sward



y = 0.00001 - 0.96x (±0.128) r^2 = 0.82 ***

Figure E3.22

The relationship between sheep 'diet quality' derived from the proportions of herbage components in the sheep diet, and 'low sward quality' derived from the proportions of herbage components in the sward



$y = 0.00001 - 0.92x\ (\pm 0.130)\ r^2 = 0.81$ ***

responding to differences between the swards in kind rather than degree would require a greater range of swards than was available in this experiment and might call for more complex techniques for the analysis of the data such as cluster analysis or canonical variates, and a different series of measurements.

Recent work in Africa (Vesey-Fitzgerald, 1960; Lamprey, 1963; Gwynne and Bell, 1968; Bell, 1969; Jarman, 1974) and in North America (Ellis and Travis, 1975; Schwartz and Ellis, 1981) has indicated that sympatric grazing animals tend to reduce competition by exploiting the environment in different ways. Differences in diet selection, grazing behaviour and social behaviour brought about by differences in body size, mouthpart morphology and gut morphology and function are thought to lead to differences in habitat selection, grazing succession and social system (Schwartz and Ellis, 1981). It has been pointed out however (Ellis and Travis, 1975) that competition may exist among sympatric ungulates, particularly if they have not evolved together. It is obviously of importance that the extent of competition or complementarity between sympatric grazing animals is determined in order that managerial decisions regarding the use of herbage resources can be made to the best possible advantage.

Unfortunately much of the work, apart from that carried out by Ellis and Travis (1975) and Schwartz and Ellis (1981) is based on little quantitative data, particularly regarding the composition of the diet selected by animals of different sizes in relation to the structure of the sward. However rather more data is available from work carried out in Australia by Dudzinski and Arnold (1973) and Langlands and Sanson (1976), on cattle and sheep grazed together.

Both these studies suggested that the availability of herbage determined to a large extent the observed differences in the diets selected by the cattle and sheep, though neither study adequately defined availability. In both of the above studies diet selection was more sensitive to variation in herbage mass in the cattle than in the sheep, the sheep selected diets consistently higher in green herbage and in-vitro OMD and differences were greatest at low herbage masses. A similar result was found in this study. Differences between the cattle and sheep in the proportions of dicots and stem in the diet were large and the differences were attributed to the animals grazing different sward horizons. Dudzinski and Arnold (1973) suggested that sheep chose to graze closer to the ground than cattle and thus obtained diets higher in clover than the cattle, particularly on short swards. Apart from some rather general descriptions by Bell (1969) of the horizons in the sward grazed by different species there appear to have been no previous investigations into this aspect of grazing behaviour. In the present Experiment 3 large differences in the botanical composition of the cattle and sheep diets occurred on the taller swards. Differences in the proportion of green material in the diet and OMD were large on very short swards. In the first instance the differences were due to the animals grazing different horizons whilst in the second the results reflect the inability of the cattle to avoid grazing the surface horizons of short swards which in Experiment 3 contained high proportions of dead material. The greater selective ability of the sheep allowed them to avoid to a large extent the dead herbage.

The differences between the cattle and sheep in the diets selected can be related to the horizons in which grazing takes place.

There is general agreement (Bell, 1969; Ellis and Travis, 1975; and Sinclair, 1980) that smaller animal species tend to have narrower muzzles, an adaptation which allows the animals to be more selective than larger species. In Experiment 3 it was suggested that the sheep were able to penetrate deeper into the taller swards, below the flower stem horizon, and select components that the cattle could not reach. Schwartz and Ellis (1981), whilst agreeing with this finding in general, suggested that diet overlaps are greater between the domesticated cattle and sheep than between undomesticated bison (Bison bison) and pronghorn antelope (Antilocarpa americana) and concluded that the domestication of sheep has made them diet and habitat generalists despite their relatively small size. The results of the present experiment suggest that this may well be true, particularly with regard to the OMD of the diets obtained (Table E3.6), where relatively few differences between the animal species were found.

The influence of body size on diet selection in grazing animals has been discussed in some detail by a number of authors (Gwynne and Bell, 1968; Bell, 1969; Schoener, 1971; Jarman, 1974; Jarman and Sinclair, 1980; Schwartz and Ellis, 1981) but the data base is limited. The general theory suggests that small ruminants should select diets that maximise nutrient intake, since they have higher metabolic rates than large ruminant species. What evidence there is would suggest that this is achieved by maxmimising nutrient concentration rather than maximising rate of herbage intake. The evidence suggests that this is generally true for domesticated species as well as wild species (Gwynne and Bell, 1968; Dudzinski and Arnold, 1973; Jarman, 1974; Langlands and Sanson, 1981). The results of the present study confirm these findings, but the conclusion must be that the strategy practised by the sheep, though enabling nutrient concentration to be relatively constant throughout the year, may prevent the animals from obtaining maximum intakes during the summer months when sward conditions reduce the accessibility of particular components. The cattle do not apparently attempt to maintain a constancy of nutrient concentration, but rather attempt to maximise rate of intake. Unlike the sheep, cattle rates of intake show a significant increase with increasing sward height. Variations in sward height appear to influence the grazing tactics of the cattle and sheep rather differently. Generally increases in sward height enable cattle to maximise rate of intake; in contrast, and particularly on very tall swards, increases in sward height may lead to some restriction of the herbage intakes of sheep as the animals increase selectivity in order to maintain the nutrient concentration of their diets, particularly since the increase in sward height is generally a consequence of stems which the sheep generally avoid.

Swards of poor quality tend to be short and to have high densities of dead herbage, as a result intakes per bite are low, but rates of biting and grazing time increase. On these swards sheep are able to select diets that provide satisfactory levels of OMD and consequently intakes are little affected. Cattle, on the other hand, require absolutely greater intakes which the animals may not be able to obtain. Under these circumstances the cattle might be expected to move to areas of vegetation which are taller, though not necessarily of greater quality. Though there is an advantage to the sheep gained by maximising nutrient intake in conditions of low herbage quality, when herbage quality is high, concentrating activity reduces the rate of intake and thus the sheep do not utilise the full potential of the vegetation.

Conclusions

The ingestive behaviour of the animals allowed them to follow grazing strategies typical of animals of comparable body size. The cattle maximised rate of herbage intake, where conditions allowed, by increasing intake per bite and compensating for declines in intake per bite by increasing rate of biting. The sheep also increased intake per bite in favourable conditions but, unlike the cattle, responded to changes in herbage density by altering daily grazing time. At sward heights below 5 cm and where the proportion of green material in the sward was less than 30% the cattle, in particular, and the sheep had low diet digestibilities, low intakes per bite and low herbage intakes.

The consequences of the grazing strategies of the cattle and sheep in the context of animal production from hill vegetation are that sheep are able to maintain nutrient intakes better than cattle at those times of year when requirements are greatest and the overall herbage quality is lowest, namely during late pregnancy and early lactation in early spring. Cattle are unable, in general, to maintain nutrient intakes when herbage quality is low, due to the reduced rate of intake, and are obliged to rely on previously adequate nutrition in the form of fat reserves. Sheep are unable to maximise intakes in summer swards as their grazing strategy still demands that they maximise nutrient concentration even when herbage quality is high.

There are consequences regarding the management of the vegetation that arise from the tactics of the grazing animals. To maximise herbage intake by the sheep in the summer months, sward conditions that allow the sheep to maximise rate of intake rather than allowing the animals to attempt to maximise nutrient concentration are required. The results of the present study suggest that a reduction in sward height alone may be sufficient. To an extent this is achieved on Agrostis-Festuca swards by the heavier stocking rates that such swards attract. In other situations with other grass communities the reduction in sward height might be achieved by a combination of grazing treatments involving cattle, such as pregrazing the swards or co-grazing. The results of Experiment 2 suggest that under intensive grazing management or where swards are intensively grazed such as reseeds in hill vegetation mixed stocking may result in greater herbage utilisation than might be under single species grazing.

The responses of the cattle and sheep to structural sward variates such as sward height were similar across the range of swards, whilst for other sward variates such as certain botanical components, the animals' responses were sward specific, indicating that the structure of the swards was largely independent of botanical description of the swards. The major determinants of herbage intake, intake per bite and rate of biting were both strongly influenced by sward height, which varied between swards as a result of season and grazing management. The effects of sward height on intake per bite and rate of biting requires further investigation particularly on taller indigenous swards where the evidence suggests a response more typical of animals grazing tropical swards may occur. The reason for the apparent difference between the structure and botanical composition of the swards in the responses given by the animals also requires further investigation.

In general the sheep appeared better adapted to grazing of hill vegetation than the cattle. They selected a diet higher in OMD than the cattle, particularly when the sward quality was at its lowest, and they were able to alter their intakes per bite, rates of biting and grazing times more successfully than the cattle in the face of changes in sward conditions. The cattle were however able to maximise their rate of herbage intake during the summer months and were able to obtain diets of comparable digestibility. It is suggested that cattle provide a useful means of managing the vegetation during the summer months at no disadvantage to themselves and some large advantage to the sheep.

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