GRAZING ECOLOGY OF GOATS, RED DEER AND SOUTH AMERICAN CAMELIDS

by

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For Calvin and the boys.

Table of Contents

List of Tables

List of Figures

For Calvin and the boys

Declaration

This thesis was composed by myself, and none of the work therein has been presented in any previous applications for a degree.

All sources of information are shown in the text and listed in the references. All help given by other people is indicated in the acknowledgments.

Mariecia D. Fraser

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Abstract

A study was undertaken to determine and compare the grazing ecology of goats, red deer and South American camelids when pastured on three contrasting vegetation types typical of hill and upland ecosystems in Scotland: an established sown sward (*Lolium perenne* dominated); an indigenous grassland (*Nardus stricta* dominated); and a dwarf-shrub community (*Calluna vulgaris* dominated). Plots at each site were grazed in sequence with data collected during one spring (May/June) and two summer (August/September) experimental sessions. For each period at each site plant species composition, canopy structure and herbage biomass were characterized. Samples of the diet selected by up to five mature castrated goats, red deer and guanacos fistulated at the oesophagus were used to establish diet composition and *in vitro* digestibility of the diet. Herbage intake and diet digestibility of an additional five intact animals of each species were determined using n-alkane faecal markers. Total grazing time was estimated using vibracorders and bite rate data collected by observation. The influence of vegetation type and season on the diet composition and ingestive behaviour of each species was evaluated. Between species comparisons on each vegetation type were also made. Differences in selectivity for and against vegetation components indicate that guanacos are principally grazers while goats and red deer are intermediate feeders. On the Lolium sward the goats and red deer selected green leaf of both monocotyledonous and dicotyledonous plants whereas the guanacos selected only graminoids. On the Nardus community the main dietary component for all three animal species was broad-leaved grasses selected from the species-rich intertussock areas. On the dwarf-shrub community there was strong selection for and against graminoid species and *Calluna vulgaris* respectively, with the dominant species of plant only making a substantial contribution to the red deer diet. Where differences between estimates of diet digestibility were identified the digestibility of material consumed by each species of animal on the sown sward was higher than that from either indigenous community; and the digestibility of material selected from the indigenous grassland was higher than that from the dwarf-shrub community. Only the *in vitro* digestibility of diets selected from the Calluna community was subject to a consistent seasonal effect. Organic matter intake for the red deer was relatively constant. In contrast, intake for the goats and guanacos was found to vary according to vegetation type, with consumption highest on the indigenous grassland community and lowest on the dwarf-shrub. When expressed per unit metabolic weight the organic matter intakes of the three species were generally similar. Total grazing time for the goats was lower than that for either the red deer or guanacos. In contrast, no consistent differences in total grazing times between the red deer and guanacos were found. The influence of differences in morphology and digestive physiology on the results obtained is explored and the implications of differences in diet composition and ingestive behaviour for sward responses and optimum grazing management regimes discussed.

CHAPTER ONE

INTRODUCTION

Introduction

In Scotland the land cover is dominated by indigenous vegetation (M.L.U.R.I., 1993), and until recently sheep production has been the main source of income on Scottish hill farms. However hill vegetation has low nutritional value for livestock (Hodgson and Eadie, 1986), especially in winter, and the costs of wintering on lower ground or supplementary feeding together with changes in the eligibility and level of government assistance make the economics of hill sheep farming at present insecure. Consequently interest has grown in the potential of integrating alternative species of livestock, such as goats (*Capra hircus*), red deer (*Cervus elaphus*) and South American camelids, into traditional production systems (Wright, 1993).

Goats are a source of fine fibre and there has been particular interest in the potential for cashmere production in recent years (Russel, 1993a). In contrast to wool and mohair, cashmere quality appears to be insensitive to non-genetic factors (Russel, 1993b). As a result predictable and constant quality cashmere could potentially be produced from even poor-quality land resources in climatically harsh regions.

Others have looked to red deer as an alternative means of using poor hill land, either farmed for venison production or managed for stalking (Blaxter *et al.*, 1974; Wilson, 1985). Pressures from afforestation, agriculture and recreation have modified the distribution of the wild population of red deer (Mitchell, Staines and Welch, 1977) with the result this species has been forced to demonstrate its ability to adapt and survive on poorer-quality, more remote and exposed hill land.

Like goats, South American camelids are a potential source of fibre for commercial production. The undercoat of the guanaco (*Lama guanicoe*) is comparable in fibre diameter and value to cashmere (Russel, 1993a) and appears to have potential as a luxury fibre. Recent work investigating the relationship between level of nutrition and fibre growth of camelids suggests that nutrition has neither a quantitative nor qualitative effect on fibre production (Russel and Redden, 1994). Thus again there is the potential for fine fibre enterprises to be based on poorer-quality vegetation without productivity being compromised.

The change from traditional livestock enterprises to those incorporating so-called 'novel' species of animal such as goats, red deer or South American camelids will require the development of new systems of management. However, little is currently known of the diet selection, herbage intake or ingestive behaviour of these three species of animal in the context of hill vegetation in Scotland, and consequently the scientific basis for their uptake in the current climate of diversification and changing land use is limited.

In addition to providing resources for commercial enterprises the hills and uplands are a rich source of wild flora and fauna (Ratcliffe and Thomson, 1988). Effective wildlife management requires a basis on which to judge the ecological carrying capacity of a particular habitat in relation to a given animal species (Caughley and Sinclair, 1994). Wild populations of red deer, which concern a wide section of the general public as an aesthetic feature of the Scottish Highlands, currently exceed the carrying capacity of the land they occupy (Callander and MacKenzie, 1991) yet there is a dearth of relevant information with which to formulate appropriate management regimes (Clutton-Brock and Albon, 1992).

New management systems must also take into account environmental factors. Reviews list many examples where foraging by goats (Campbell, Ebersohn and Broembsen, 1962) and red deer (Mitchell, Staines and Welch, 1977) have been associated with the deterioration or destruction of vegetation resources. However, in many cases the problem is caused or exacerbated by man's mismanagement. In contrast, an understanding of the foraging strategy of sheep and cattle can now be used to predict the impact of these species on vegetation dynamics (Hodgson, 1985a). The lack of information regarding the grazing ecology of goats, red deer and South American camelids on semi-natural communities in the UK limits opportunities to manage and utilise these alternative species to achieve conservation as well as agricultural objectives in these ecosystems.

Comparative information on diet selection and nutrient uptake of these species would also contribute to the general understanding of the grazing strategies of ungulate species. Historically, foraging theory has focused specifically on predators and parasitoids (Pyke, 1984; Stephens and Krebs, 1986). Only relatively recently has there been interest in adapting conventional understanding of an animal's response to its environment's heterogeneity to incorporate choices made by herbivores (Owen-Smith and Novellie, 1982; Illius and Gordon, 1987; Ungar and Noy-Meir, 1988; Lundberg and Astrom, 1990a). This interest has in turn led to a variety of studies quantifying plant/animal interactions and specifically the effect of vegetation characteristics on the mechanistic processes that underlie diet selection and ingestive behaviour. In general these experiments generate data under very controlled conditions with animals consuming one plant species from an artificial sward (Black and Kenney, 1984; Laca *et al.*, 1992; Gross *et al*, 1993). If an animal's response under more complex grazing systems is to be predicted and understood, detailed comparative information regarding diet selection and ingestive behaviour on a range of vegetation types is required.

Differences in diet selection and ingestive behaviour of sympatric wild or free-roaming ungulates have been related to differences in body size, mouth size and method of prehension and digestive tract morphology (Hofmann, 1973; Jarman, 1974; Schwartz and Ellis 1981; McNaughton, 1984; Illius and Gordon, 1987; Gordon and Illius, 1988). However, as a rule such animals inhabit heterogeneous ecosystems and have access to a variety of vegetation types. Consequently opportunities to collect comparative information on diet selection and nutrient intake by different animal species when restricted to one vegetation community are limited.

This study was set up to determine and compare the grazing ecology of goats, red deer and South American camelids on three contrasting vegetation types typical of the hills and uplands of the UK: an established sown sward (*Lolium perenne* dominated); and indigenous grassland community (*Nardus stricta* dominated); and a dwarf-shrub community (*Calluna vulgaris* dominated). This research complements previous work which established baseline information on the diet selection (Grant *et al.*, 1985; Grant *et al.*, 1987), herbage intake and ingestive behaviour (Hodgson *et al.*, 1991) of cattle and sheep confined to comparable vegetation communities.

CHAPTER TWO

REVIEW OF GRAZING ECOLOGY

2.1 INTRODUCTION

To meet its requirements for maintenance, growth and reproduction an animal must gain energy and nutrients through consumption of food. For a grazing animal there are few situations where there are not qualitative or quantitative limitations on the food items available for consumption (Hodgson, 1982a). Consequently the intake of this animal is likely to be constrained by either digestive capacity; i.e. the product of the volume of the organ(s) used for the breakdown of plant tissue, and the digestive turnover within the organ(s) (Belovsky, 1986); or feeding time (Bunnell and Gillingham, 1985). By modifying aspects of its ingestive behaviour an animal can counteract these constraints and increase the probability of meeting its nutrient requirements from the available vegetation. However, feeding must be integrated with additional tasks necessary for survival and reproduction. Consequently time and energy may need to be partitioned between a number of activities. The approach generally applied to the study of feeding strategies, optimal foraging theory (Pyke, 1984), assumes that animals maximise some objective function, usually energy captured per unit time, by choosing among alternate behaviours subject to a set of constraints (Stephens and Krebs, 1986).

This review will describe the different ways in which an animal can modify its behaviour to allow it to meet its requirements within the constraints imposed by the food resource available. It will then consider the physiological and morphological features of a given animal species which are influential in determining which of these options are chosen.

2.2 MEETING REQUIREMENTS

2.2.1 Diet selection

Carnivores, granivores and fugivores can recognise and select food items with a relatively high degree of precision since they prey upon food items which occur as discrete packages (Stephens and Krebs, 1986). In contrast, large mammalian herbivores select food items from a structurally and chemically diverse spectrum and consequently discerning the nutritional merits of individual food items is more difficult. Thus, whereas the food source for carnivorous predators can be characterised as being patchily distributed, highly nutritious and mobile, that of a herbivore will be typified by the nutrients being at low density (Westoby, 1978) and, particularly on intensively managed sown swards, more evenly distributed (Senft *et al.*, 1987; Gordon and Lascano, 1994). However, despite this relative uniformity in food distribution for the herbivore, a degree of variation will exist between individual dietary items in type and/or amount of nutritional constituent which may be exploited.

Selection of dietary components can be thought of as occurring at a number of hierarchical levels (Jarman and Sinclair, 1979; Senft *et al.*, 1987). Firstly, in a given feeding bout an animal can choose a vegetation type or community on which to feed. This decision may be influenced by factors such as climate, topography and the availability of shelter (Arnold, 1984; Stuth, 1991) in addition to forage quality and quantity. Secondly, within a vegetation type or community an animal can choose among plant types or species to eat. Thirdly, it may choose which morphological units of those plants to eat. Depending on the choices made by a given animal, the composition of the diet selected may be substantially different to the proportions of various species or plant parts present within a particular community or sward (Arnold, 1960a; Grant *et al.*, 1985). Such selection minimises the adverse effects of pronounced seasonality in the quality and quantity of the food available for selection (Milne, 1974; Jarman and Sinclair, 1979; Grant and Hodgson, 1986). Clearly, the scope for selection will depend on the heterogeneity of the vegetation the animal is feeding from and the spatial distribution of different plant components, and for domesticated species this is generally dictated by management regimes imposed by man (Gordon and Lascano, 1994).

The sown swards typical of intensive production systems are generally characterised by being highly digestible and consumption is more likely to be limited by quantity than quality of vegetation available (Hodgson *et al.*, 1991). In comparison indigenous plant communities are rarely limiting in overall vegetation quantity. However, such swards are generally characterised by a wide diversity of plant species which may offer extremes in digestibility (Grant and Campbell, 1978; Armstrong, Common and Smith, 1986; Gordon, 1989a). Through selection of particular plant species or plant parts an animal may exploit this variation and consume a diet higher in quality than the average for the environment. To date the majority of studies on indigenous vegetation have considered diet composition at the community or mosaic level. However, such areas of vegetation are composed of a variety of plant species and morphological units, and without an insight into within-community selection the understanding of the animal's response to the vegetation available which is gained is comparatively superficial.

In addition to the digestibility of different plant species within vegetation communities, their spatial distribution (Spalinger, Hanley and Robbins, 1988) and seasonality of plant growth (Arnold, 1960a; Arnold, Ball, McManus and Bush, 1966; Gordon, 1989a) are likely to be limiting to nutrient intake and result in the uneven distribution of grazing pressure both within and between plant communities (Hunter 1962; Jarman and Sinclair, 1979; Grant and Maxwell, 1988; Gordon, 1989b). In such circumstances, utilisation of a given species may be dependent on the availability of another, more preferred species (Milne, Bagley and Grant, 1979; Grant and Hodgson, 1981; Vulink and Drost, 1991). If the density of a preferred species is too low or it is too widely dispersed then although it will be consumed if encountered, there may be no benefit to the animal in searching for it. Clearly, without a comprehensive characterisation of the vegetation on offer interpretation of an animal's response to different components within the sward is impossible, yet few studies of plant/animal interactions on heterogeneous swards include detailed botanical measurements at the plant species or plant part level.

In addition to diversity in nutritional quality of different species of plant, variations are found in the digestibility of different morphological units of a single plant and between live and dead components (Grant and Campbell, 1978). There is general agreement that from the single plant a herbivore will consume leaf in preference to stem, and green (or young) in preference to dry (or old) (Arnold and Dudzinski, 1978). This selection of particular plants or plant parts results in the material eaten usually being higher in nitrogen and gross energy but lower in fibre (Arnold, 1960a) than the material offered and rejected (Cowlishaw and Alder, 1960).

Of equal importance to selection for particular components within a sward is selection against. Selection or avoidance of particular plant species or plant parts may be influenced by various types of plant defence. The form and function of animal repellent characteristics of plants which may be encountered are diverse and include: physical deterrents such as form or growth habit (Flores, Provenza and Balph, 1989) and barbs or thorns (Cooper and Owen-Smith, 1986); high fibre contents and slow fractionation rates which lead to low digestibility (Lundberg and Astrom, 1990b); and chemical toxicity (Freehand and Janzen, 1974). However, the contest between plant and animal is an on-going process (Rhoades, 1985) and adaptive features to counteract the effectiveness of such plant defences can be found. For example, a number of animals including goats (Provenza and Malechek, 1984) and deer (Austin *et al.*, 1989), may minimise the effects of plant secondary compounds by producing salivary mucoproteins which bind specifically to plant tannins and nullify their digestion-inhibiting effects (Robbins *et al.*, 1987).

Vertical selection for different elements has also been identified within sown swards. Consumption of grass and clover by sheep has been linked to their proportions in the grazed horizon (Milne *et al.*, 1982), while Barthram (1980) found grazing to be confined to the layer which contains only green leaf material. This led to the suggestion that layers containing leaf sheath inhibit grazing and limit the depth of the grazed layer, even when the consequence is a marked reduction in herbage intake. The comparatively undetailed botanical measurements generally associated with grazing trials on indigenous communities has meant comparable data from heterogeneous vegetation is scarce.

In all situations the relationship between the animal and the vegetation it is feeding upon is dynamic (Lundberg and Astrom, 1990a). Biomass extraction through ingestion to provide energy/nutrient gain for an animal removes material from a number of pools of photosynthetic mass and may alter the subsequent growth form of individual plants (Pellew, 1983; Ward and Saltz, 1994). Thus through consistent selection the animal may alter the composition of the sward or community (McNaughton, 1984). An understanding of the foraging strategies of cattle and sheep can now be used to predict the impact of these species on vegetation dynamics (Hodgson, 1985a). However, comparative information for a range of animal species is required to achieve greater flexibility in the options available to those attempting to manage temperate grazing systems, whether to meet agricultural or conservation objectives.

2.2.2 Intake

As indicated earlier, herbage intake can be a major factor dictating nutrient intake, and can vary fivefold depending on sward conditions (Hodgson and Grant, 1981). In particular it is likely to be the primary source of variation in nutrient intake rate on intensively managed sown pasture (Penning 1986). In turn the intake rate of any given component will be dependent upon the potential rate at which it can be eaten, its accessibility, and its palatability, i.e. those factors inherent in a food item which elicit a selective response by the animal.

The relationship between forage intake rate and availability is characterised by a functional response (Holling, 1959; Spalinger, Hanley and Robbins, 1988; Lundberg and

Astrom, 1990a; Gross *et al.*, 1993). In order to understand the cause-effect relationships between sward characteristics and intake it is necessary to know how the components of sward structure influence the mechanics of the grazing process (Hodgson, 1985b). The bite is the most important determinant of intake rate (Stobbs, 1973; Hodgson, 1985b; Spalinger, Hanley and Robbins, 1988). The mass of an individual bite taken by an animal is determined by the bite area and the bite depth; the product of which is the bite volume (Burlison, Hodgson and Illius, 1991); and the mass of herbage per unit volume in that space.

The realisation that sward height is a key component affecting intake rate has led to its control becoming a widely used management tool (Hodgson, Mackie and Parker, 1986). Bite mass has been found to decrease with decreasing sward surface height, and, in order to try and maintain intake rate bite rate may be increased (Allden and Whittaker, 1970; Penning 1986). At the same time, prehending bites account for an increasing proportion of total jaw movements in response to a decrease in mass per unit area (Black and Kenney, 1984; Penning, 1986). Conversely, a reduction in biting rate on taller swards is associated with an increase in masticating rate (Penning, 1986).

Sward bulk density, a low stem content and a high leaf/height ratio have also been identified as having a major influence upon the size of bite taken (Stobbs, 1973). However, Black and Kenney (1984) found the relationship between intake rate and the combined representation of sward height and bulk density, herbage mass, more consistent. More recent work has further developed the methodology of Black and Kenney (1984) for measuring independent effects and interaction of sward structural characteristics on bite dimensions and bite mass (Ungar, Genizi and Demment, 1991; Laca *et al.*, 1992). This work has confirmed bite mass cannot be predicted solely on the basis of herbage mass; both sward height and density must be taken into account. Sward height, bulk density and mass per unit area, separately, explained seventy-one per cent, twenty-eight per cent and eighty-eight per cent of variance in bite mass respectively (Ungar, Genizi and Demment, 1991). With the relationship between herbage intake and sward structure the subject of so many different investigations a profusion of empirical results exists and mathematical modelling is now being used to integrate the morass of data generated (Ungar and Noy-Muir, 1988; Demment and Greenwood, 1988).

Daily intake is the product of instantaneous intake rate and the total duration of grazing bouts, i.e. grazing time. However, unacceptable errors are likely to be encountered if short-term estimates are extrapolated to free-roaming animals (Penning *et al.*, 1991; Laca *et al.*, 1992). For example, bite rate tends to be overestimated when measured over periods shorter than two minutes, particularly on swards that enable large bite weights to be taken (Forbes, 1988).

The wider applicability of such work is also limited by the homogeneity of the vegetation resource used during such trials. To date the majority of intake studies have concentrated on relatively uniform sown swards or artificial swards. As a result they have only considered vertical variation and density within the sward. Indigenous swards are characterised by intimate mixtures of plant species and morphological units. The spatial relationships between plant species or morphological units may limit intake in mixed sward/community situations.

2.2.3 Grazing Time and Pattern

As instantaneous intake rate and grazing time together determine daily intake rate an animal can alter its intake by adjusting time spent grazing. An increase in grazing time in response to limitations imposed by herbage availability has been recorded for sheep (Allden and Whittaker, 1970). However, the associated compensation became increasingly more incomplete as herbage mass or height declined. Likewise cattle have been found to be unable to satisfy their feed requirements on high-quality but lowyielding swards, despite increasing grazing time to compensate for the small bites prehended (Chacon, Stobbs and Dale, 1978). Such increases in grazing time have been found to be associated with a decrease in ruminating time (Arnold, 1960b; Penning, 1986).

Grazing time is the product of the number of feeding bouts and length of those bouts. Currently the mechanisms that control the initiation and termination of grazing are poorly understood. Nevertheless, a number of factors which influence overall grazing time and/or grazing pattern have been identified, including environmental conditions (Stuth, 1991) and group size (Penning *et al.*, 1993). Grazing activity patterns are also correlated with body size (Bunnell and Harested, 1989) and diet. Selective feeders were found to graze more frequently and less intensively, most likely as a result of the more rapid digestion and passage of higher quality foods (Schwartz and Ellis, 1981).

Characteristics of the vegetation being selected from dictate the proportions of time spent engaged in the different components of ingestive behaviour (Bunnell and Gillingham, 1985). Thus if an animal is foraging in food saturated patches the processes of cropping and chewing are the principal factors (Spalinger and Hobbs, 1992). In contrast when foraging in food dispersed patches cropping and searching will limit intake rate. This allocation of more grazing time to searching leads to an overall drop in bite rate where food items are dispersed (Stuth, 1991)

2.3 MORPHOLOGICAL AND PHYSIOLOGICAL FEATURES INFLUENCING DIET SELECTION AND INGESTIVE BEHAVIOUR

2.3.1 Age and physiological status

The nutrient requirements of a given animal are not fixed but are affected by factors such as age and/or physiological status. As a result changes in diet selection or herbage intake may be observed (Arnold and Dudzinski, 1967; Langlands, 1968) as an animal alters its foraging strategy to accommodate new demands for energy or specific nutrients. Even when nutrient requirements remain constant other factors may alter and impose constraints on how these requirements are met, again affecting the foraging strategy of the animal concerned. For example, although herbivores generally fall into the category of "energy maximisers" (Westoby, 1978; Demment and Van Soest, 1985; Vulink and Drost, 1991), during the breeding season a dominant male may appear to be a "time minimiser", attempting to satisfy its minimum energy requirements in the least feeding time in order to increase mating opportunities while females and non-reproductive males remain energy maximisers (Belovsky, 1986).

2.3.2 Body size

Body size has a fundamental effect on the foraging strategy of an animal since this and related variables determine the overall time-energy constraints within food must be secured. In particular there is a strong relationship between body size and metabolic requirement (Brody, 1945; Kleiber, 1961). In general the food requirements of mammals increase with increasing body weight as a result of increasing costs of maintenance and production, although significantly this increase is not linear (Demment and Van Soest, 1985). Consequently, although larger mammals require more nutrients per day than smaller mammals their relative requirements are lower. Thus a larger ruminant requiring a greater absolute quantity of nutrients during a day will have less time per unit of nutrient to spend selectively foraging than does a smaller ruminant with a lower absolute requirement (Bell, 1970; Jarman, 1974), and large ungulates have been found to abandon selective grazing under conditions where it is still profitable for small ungulates to continue selective grazing (Schwartz and Ellis, 1981). Likewise, larger animals may be forced to move to taller, more accessible parts of the sward or graze other communities once preferred areas have been grazed too short to allow intakes to be maintained (Clutton-Brock, Iason and Guiness, 1987; Illius and Gordon, 1987).

However, since the larger animal has a lower relative requirement it can in general meet its nutritional needs with relatively lower quality forage (Illius and Gordon, 1991). In addition, increasing body size should theoretically produce higher digestibilities because of longer retention times (Van Soest, 1982). This relaxation in the constraints of rapid passage, together with the greater metabolic requirements of large animals, has been suggested as a prerequisite for the evolution of gut structures that selectively delay the passage of fibrous foods (Demment and Van Soest, 1985). In practice, however, the increase in digestibility of a given food with increasing body size has been found to be negligible (Illius and Gordon, 1991).

2.3.3. Mouth morphology

Mouth size and body size are highly correlated, presumably because of the overall time-energy constraints on forage selectivity. Consequently, small ungulates tend to have mouths adapted for carefully selected discrete high quality food items while large species have mouths adapted for rapid ingestion of large quantities of undifferentiated items, possibly of low quality (Jarman and Sinclair, 1979). More specifically the dimensions of the incisor arcade determines the extent to which an animal can prehend and ingest discreet food items from within the spatial array of vegetation (Grant *et al*, 1985; Gordon and Illius, 1988; Flores, Provenza and Balph, 1989), and consequently determines the degree of selectivity that is mechanically possible for the forager to exhibit, and the time and energy costs of selectively foraging on specific plant parts or individuals.

Differences can be identified in the dentition of grazers and browsers, with the two categories having incisor arcades which are typically broad and flat or narrow and pointed respectively (Gordon and Illius, 1988) while roughage eaters which graze and ruminate for relatively prolonged periods each day have well-developed chewing muscles and molar arcades (Axmacher and Hofmann, 1988). Likewise morphological and functional characteristics of associated anatomical parts, such as lips, tongues and salivary glands, can be related to feeding type (Hofmann, 1989) and may enhance the ability of the herbivore to prehend, ingest or masticate food.

2.3.4 Digestive system

Two distinct digestive systems have evolved in herbivores which differ in the location of the fermentation site and the existence of a rumination process. All three of the species studied during this series of experiments can be considered to have ruminant digestive systems. In comparison with a hind-gut digestive system this is hypothesised as having two principal advantages. Firstly, regurgitated boluses can be chewed repeatedly thus allowing the food to be ground to a smaller particle size without compromising ingestive rate, and secondly structurally complex carbohydrates such as the cell walls of plants are digested by microbes in the reticulo-rumen before entering the true stomach (i.e. the omasum and abomasum). The principal disadvantage of ruminant digestive systems is that in order for food to pass from the rumen into the rest of the digestive tract it must be broken down to a relatively small particle size. Consequently the selective retention of very fibrous forages limits the rate of food passage through the gastrointestinal tract of the ruminant and restricts consumption of additional forage (Blaxter, Wainman and Wilson, 1961; Campling, 1964). Intake is, therefore, controlled by the capacity of the alimentary tract and in particular the reticulo-rumen. In contrast, a hind-gut digestor may be less efficient at digesting the fibrous cell walls of plants but can pass much more plant material through its digestive tract daily and thus extract more nutrients than would a ruminant on fibrous plant material (Janis, 1976; Duncan et al, 1990; Illius and Gordon, 1992).

The digestibility of the cell wall fraction of a forage is a function of the digestion rate acting on a particle for the duration of its retention within the gut. Therefore, in order for an animal to benefit from a high fibre diet, food must be retained within the rumen for a sufficient time to digest the cellulose component of the fibre (Van Soest *et al.*, 1983). For an animal with a relatively small rumen, rumen fill is reached in a relatively short time during feeding and consequently voluntary intake would be greatly restricted on a high cellulose diet. Thus a high rumino-reticular volume relative to body weight is an adaptation to a high-cellulose diet, typically a diet consisting primarily of grasses. In contrast, low rumino-reticular volume to body weight ratio is an adaptation to a low cell-wall diet typically consisting primarily of young grasses, forbs or browse (Prins and Geelen, 1971; Demment and Longhurst, 1987).

This relationship between feeding behaviour and gut morphology formed the basis of a classification system (Hofmann, 1968) which categorised ruminants as belonging to one of three groups: concentrate feeders; grass and roughage feeders; and seasonally and regionally adaptable intermediate feeders (Hofmann and Stewart, 1972; Hofmann, 1973). According to this classification, concentrate feeders prefer to browse on rapidly digested leaves, shoots and fruits and have a characteristically small rumen and omasum but relatively large reticulum. In contrast, grass and roughage feeders which can survive on bulky fibrous diets have a large rumen and omasum but small reticulum. Differences were also identified in the internal structure of the stomach compartments and the mucosal surface formations in the various regions of the stomach (Hofmann, 1968; Demment and Longhurst, 1987). Intermediate feeders, which appear to be adapted to mixed habitats and can accommodate extreme climatic conditions and seasonal changes in plant fibre content, were reported as exhibiting characteristics between those of concentrate and roughage feeders (Vrba, 1984). However, the functional relationships between gut structure and digestive strategy inferred by Hofmann (1973, 1989) do not appear to bear up to detailed analysis (Gordon and Illius, 1994).

While the detailed anatomical information available for a wide range of wild, semi-domesticated and domesticated species of animal has been used to predict their response to broad categories of vegetation, the potential for using differences in diet selection and niche separation identified in this way as a management tool for manipulating grazing systems has been largely ignored.

2.4 SUMMARY

1. By selecting particular plant species and/or plant parts an animal can consume a diet of higher nutritional value than the average on offer from the vegetation available.

2. Herbage intake and associated aspects of ingestive behaviour such as bite size, bite depth and grazing time may also be modified to accommodate changes in vegetation quality and/or quantity.

3. The response of a particular species of animal to a given situation can be predicted from morphological and functional adaptations.

4. Most studies have considered plant/animal interactions on homogeneous sown swards, and consequently their results have limited relevance for natural plant communities.

5. Previous studies on indigenous vegetation types have generally incorporated mosaics of differing plant communities, whereby animals' diet and intake are integrated across communities. Consequently detailed within-community comparisons have not been possible.

6. Differences in vegetation community selection by free-ranging animal species have limited interpretation of between-species differences in diet composition and intake.

CHAPTER THREE

MATERIALS AND METHOD

3.1 SITES AND MANAGEMENT

To allow a close comparison with equivalent data for conventional livestock species to be made, the basic experimental design followed that of a series of experiments investigating seasonal variation in diet selection, herbage intake and ingestive behaviour of sheep and cattle grazing specified plant communities (Grant *et al*, 1985; Grant *et al*, 1987; Hodgson *et al*, 1991).

The goats, red deer and guanacos studied grazed three contrasting vegetation communities encompassing extremes in structure and quality; a *Lolium perenne* dominated established sown sward; a *Nardus stricta* dominated indigenous grassland community; and a *Calluna vulgaris* dominated dwarf-shrub community. The Lolium and Calluna experimental sites were located at the Macaulay Land Use Research Institute's Glensaugh Research Station (Laurencekirk, Kincardineshire; National Grid reference NT 670800); and the Nardus experimental site at the Institute's Sourhope Research Station (Yetholm, Roxburghshire; National Grid reference NT 840210).

On each indigenous community two adjoining experimental plots of approximately 3 ha were constructed; while on the more productive ryegrass sward the plots were 1 ha each. The plots on the Nardus and Calluna communities were located on vegetation which had previously been incorporated within large hill enclosures. Consequently management had been minimal and typical of farming regimes in marginal areas. The Lolium sward was also representative of its type, and had received routine applications of nitrogenous fertiliser and herbicides. Outwith the experimental periods the plots on all three vegetation types were grazed by farm livestock; primarily sheep in the case of the Nardus area and deer in the case of the Lolium and Calluna areas. In the case of the Nardus and Calluna plots representative utilisation was maintained by opening gates in the perimeter of the experimental area and incorporating these once again in the large hill enclosures. All livestock was excluded from the experimental sites for at least four weeks prior to each grazing trial. This period of growth in conjunction with the previous period of typical utilisation ensured that while representative botanical composition and canopy structure were maintained the experimental animals were not restricted by quantitative limitations in the overall biomass of vegetation available.

3.2 EXPERIMENTAL DESIGN

During the growing seasons of 1991 and 1992 the experimental sites were grazed such that information was collected from a summer trial in 1991 and from a spring and a summer trial in 1992, allowing an assessment to be made of seasonal changes in the response of the three species of animal to the vegetation available. Each investigation consisted of a five-day 'run-in' period followed by a seven-day experimental period. During the former, animals gained experience of the sward on the first or 'run-in' plot while vegetation measurements to establish botanical composition, canopy structure and sward biomass were carried out on the adjoining measurement plot. Animal measurements commenced at the start of the seven-day period when the animals were moved from the 'run-in' area to the measurement area. To ensure that the direct presence of one species of animal did not modify the behaviour of another (Arnold, 1984), this second measurement area was subdivided into three subplots and a species of animal randomly assigned to each. To provide each species with access to the entire measurement area and hence make interspecific comparisons valid, the animals were rotated around these subplots on days three and five of the measurement week, effectively giving forty-eight hours on each.

Measurements of herbage intake, grazing time, grazing pattern and bite rates by five animals per species were made on each of the three vegetation types. In addition four or five oesophageal fistulated goats; three to five oesophageal fistulated red deer; and one to five oesophageal fistulated guanacos were available to estimate the botanical composition and digestibility of the diet selected by each species of animal on each community. Where possible the same animals were used throughout the project, and within a season the composition of the group was consistent.

3.3 VEGETATION MEASUREMENTS

3.3.1 Species composition and canopy structure

An extensive range of methods and techniques are available to provide a quantitative description of vegetation (Grant, 1993), depending on the particular aspects under investigation. Of these, the two approaches most commonly adopted to determine species composition of the sward within experimental plots are sample clipping and separating into botanical components, or estimating specific frequency from the intercepts of a steel pin projected through the vegetation either vertically (Welch, 1984b; Glatzle, Mechel and Vaz Lourenco, 1993) or inclined at an angle (Grant *et al*, 1985). Both methods can provide detailed descriptions of plant communities in terms of plant species, plant parts and proportions of live and dead material. However, botanical separations to species level are extremely time-consuming, particularly in the case of samples from indigenous swards. In contrast, the use of a point-quadrat method allows relatively rapid collection of data which can be used to create a comprehensive profile of the vegetation present within an experimental area. In addition by recording height from ground level of elements identified canopy structure can be characterised. One of the principal disadvantages of the point quadrat method is a bias towards plants with large and/or horizontal leaves. In addition this method can underestimate the proportion of dead material in the sward if the lower strata of the sward are too dense to record (Grant, 1993).

Over four days during the 'run-in' period botanical composition and canopy structure were characterised for each of the three vegetation communities using a point quadrat inclined at 35°. The possibility of extreme environmental conditions during this period having an impact on the sward profile generated for each plot was mediated by recording the same number of quadrats for each of the three sub-plots daily.

On the Nardus and Calluna communities each of the measurement sub-plots were partitioned into forty divisions and a quadrat measured at random within each of these. On the smaller ryegrass sub-plots twenty quadrats were taken using the same restricted randomisation procedure. For each quadrat at least twenty-five contacts were made, with the transverse of a needle always completed. This led to approximately 1200 contacts being identified per sub-plot on the indigenous communities and approximately 600 per sub-plot on the sown pasture. Data was logged using a purpose-written software program (Mark Gillingham, E.R.C.C., 1986) run on a Husky Hunter computer. For each contact plant species, state (green or dead), and morphological unit were recorded, along with height from the humus layer. Morphological units were recorded as either leaf, vegetative stem, flowerstem or flower for all plants except the heaths where current season's shoots, old growth, wood and flower were more appropriate. Preliminary analysis was carried out using a second computer program (I. Finlayson, M.L.U.R.I., 1992) to tabulate percentage specific frequency values for each data set.

Statistical analysis was carried out on proportional data following an angular transformation. Inter-plot similarities in vegetation composition were calculated using the City-block measure adjusted for double zeros. This was then used to derive and plot principal co-ordinates.

The degree of clumping of the various species encountered on each community was determined using Green's index (GI) (Ludwig and Reynolds, 1988):

$$GI = ((s^2/x) - 1) / (n-1)]$$

where x and s^2 are the mean and variance respectively, and n the number of individuals in the sample. GI varies between 0 (for random) and 1 (for maximum clumping). Unlike other indices of dispersion, GI is independent of n and is therefore more suitable for comparing across communities.

3.3.2 Herbage biomass, botanical separations and *in vitro* digestibility

Non-destructive methods of measuring herbage biomass, such as eye estimations, height and/or density measurements, and devices such as an electronic pasture yield meter (Hodgson, Rodriguez Capriles and Fenlon, 1977) are more liable to bias than cutting methods (Frame, 1981). Cutting methods also have the advantage of generating samples for additional analyses including botanical composition and *in vitro* digestibility.

Vegetative biomass was determined by collecting herbage samples from within quadrats on the final day of the 'run-in' period. Using a similar restricted random procedure to that utilised during the point quadrat data collection, six and ten quadrats per sub-plot were collected from the sown and indigenous communities respectively. In the case of quadrats on the Nardus vegetation, samples were taken from inter-tussock areas since evidence suggested these areas would be the focus of ingestive attention under the conditions of high herbage availability of this study. As such areas generally feature a variety of plant types and species, a complete picture of their composition is essential if an accurate interpretation of the animals' response to this type of heterogeneous environment is to be made. For all three communities the vegetation rooted within each quadrat site was removed at ground level using battery-powered sheep shears. The dimensions of the quadrats varied depending on the vegetation community under study. On the ryegrass plots a conventional 1220 x 150 mm quadrat was used. However on the Nardus community a smaller 400 x 200 mm quadrat was more practical since sampling was to be restricted to the inter-tussock areas. In contrast on the heather plots a larger 600 x 400 mm quadrat was used to accommodate the distinctive structure of the dominant plant species. An additional side-clip of vegetation was cut from the edge of the quadrat site and retained for determination of botanical composition and *in vitro* digestibility. All samples were stored at -20°C prior to analysis.

To determine herbage biomass and dry matter content the fresh weight of each sample was recorded. The samples were then dried at 90°C for forty-eight hours and re-weighed.

The side clip associated with each quadrat was separated into species and morphological groupings equivalent to those identifiable within the extrusa samples from the same community (see 3.4.1 Diet Composition). The Lolium sward had the smallest number of categories: green lamina of broad-leaved grasses; dead lamina of broad-leaved grasses; grass vegetative stem; grass flowerstem; grass flower and seedhead; green leaf of *Trifolium repens* ; dead leaf of *Trifolium repens*; green petiole of *Trifolium repens*; dead petiole of *Trifolium repens*; other dicotyledonous plants; and litter. Grass material within the samples collected on the Nardus community was separated into: green lamina of *Nardus stricta*; dead lamina of *Nardus stricta*; green lamina of broad-leaved grasses; dead lamina of broad-leaved grasses; green lamina of fine-leaved grasses; dead lamina of fine-leaved grasses; grass vegetative stem; grass flowerstem; and grass flower and seed head. Additional plant species which occurred were grouped according to genus and separated into green and dead categories. Unattached dead material was grouped in a litter category.

From each of the heather side-clips four to five *Calluna vulgaris* shoots were randomly selected and separated into flower; current season; green old growth; dead old growth; and wood. The remainder of the sample was then separated into the following categories: additional *Calluna vulgaris*; *Erica cinerea*; *Empetrum nigrum*; green leaf of *Vaccinium myrtillus*; dead leaf of *Vaccinium myrtillus*; green stem of *Vaccinium* *myrtillus*; dead stem of *Vaccinium myrtillus*; green leaf of *Vaccinium vitis-idaea* ; dead leaf of *Vaccinium vitis-idaea*; green stem of *Vaccinium vitis-idaea* ; dead stem of *Vaccinium vitis-idaea*; litter; and grass categories similar to those listed for the *Nardus* community.

Since estimation of *in vitro* digestibility is affected by the method of drying (Grant and Campbell, 1978), all samples were freeze-dried before being weighed to allow the proportion of each plant group in each side-clip on a dry matter basis to be calculated. The separated categories from each quadrat side-clip were then bulked for each sub-plot to provide sufficient sample for subsequent *in vitro* analysis, and milled through a 1mm sieve.

Statistical analysis was carried out on the proportional data after it had undergone an angular transformation. For each vegetation type analysis of variance was carried out to investigate the effect of session and sub-plot on herbage biomass and the contribution of each vegetation category to the overall sward.

3.4 ANIMAL MEASUREMENTS

The goats used during the project were all cashmere feral crosses which originated from the Macaulay Land Use Research Institute's main herd based at the Institute's Sourhope Research Station. All were mature castrated males. The red deer were also supplied by the Institute's commercial herd, which is based at its Glensaugh Research Station. Again all were mature castrated males. Unlike goats and red deer, South American camelids in general and guanacos in particular are not readily available in this country. Consequently the group of ten guanaco and part-guanaco mature males and castrates used during this project came from several sources. Mean liveweights of the goats, red deer and guanacos respectively over the two years were 49.4 ± 2.46kg, 102.7 ± 2.64kg and 109.0 ± 4.6kg.

Close-quarter handling and restraint of the red deer and guanacos was achieved using deer handling pens and a drop-floor crush (Ritchie's of Elgin; Hamilton, 1994). The animals were familiarised with this equipment prior to the experimental fieldwork to ensure minimal disturbance of the animals during data collection.

As outlined in the experimental design, during each experimental fortnight the animals became accustomed to each vegetation type during a five day 'run-in' period after which they were moved to the measurement area.

3.4.1 Diet composition

Although detailed observations of a given sward before, during and after grazing may suffice where the effect of grazing on sward composition and productivity is under investigation (Cowlishaw and Alder, 1960; Grant, 1993), where more detailed information is required regarding diet composition or if heterogeneous swards are being grazed animal-based methods are generally employed. These range from the relatively simplistic manual collection of herbage samples based on observation and mimicry to the use of surgically-modified animals. Which method is most appropriate for a given situation depends upon the species of animal under study, animal numbers, size of study area and vegetation type. Thus in large study areas where information on selection at the vegetation community level is sufficient data is commonly gathered by observation, usually supplemented by records of dung deposition (Welsh, 1984a; Gordon, 1989b). If the study animals can be captured and equipment fitted then radio telemetry may be used to identify and quantify use of habitats where observation methods are not practicable (Catt and Staines, 1987; Warren *et al.*, 1992).

The choice of method for determining diet composition at the plant species or plant part level is subject to similar considerations. Thus nonobtrusive observations or measurements of the utilisation of forage plants are commonly employed when studying wild animals (Parker, Gillingham and Hanley, 1993). However, such methods are subject to observer error, particularly where an assessment of the composition of a diet selected on structurally complex vegetation is required. An alternative approach is the collection of material which had been consumed by the animal. When plants are eaten most of their tissue is broken up and digested but small fragments, particularly of the epidermal cuticle remain intact and are passed out in the faeces. These particles can be identified to species or family level from their morphological features and used to determine which plants were originally selected (Crocker, 1959). However, this method does not take into account variations in rate of digestion of different plant species or plant parts (Slater and Jones, 1971). Similar limitations apply to the identification of material obtained from the alimentary tract; usually the rumen. Thus stomach content analysis and faecal analysis have been found to overestimate less digestible portions of the diet while underestimating more digestible portions (McInnis, Vavra and Krueger, 1983). Another drawback of rumen content analysis is that it generally involves the sacrifice of the study animal.

If tame wild animals are available or a domesticated species is under investigation, the most common approach is to prepare animals fistulated at the oesophagus, which allows repeated collections of relatively undigested material to be made. Questions of accuracy remain however (Jones and Lascano, 1992), as a sample collected over approximately thirty minutes by a surgically-prepared animal is assumed to be representative of the long-term diet selected by intact animals.

Using a maximum of five, mature castrated oesophageal-fistulated animals of each species extrusa samples were collected for each of the measurement sub-plots. The goat and red deer oesophageal fistulates were prepared using the techniques developed for sheep (Cook *et al.*, 1963). In the case of the guanacos, however, this basic methodology had to be refined to accommodate anatomical and behavioural differences (Goddard and

Fraser, 1994). Following successful establishment of a fistula the animals were familiarised with the sampling equipment and experimental routine.

After consideration of the lack of knowledge available regarding oesophageal fistulation in the guanaco it was decided to initially prepare only one animal to assess recovery and performance. The experience gained during this first year then contributed to the successful establishment of a further four oesophageal fistulates prior to the second year of fieldwork. The number of goat and red deer oesophageal fistulates available for sampling also fluctuated between experimental sessions as a result of a variety of health problems all unrelated to the fistulation process. Although lack of animal numbers could have been compensated for by taking repeated samples from each animal on each subplot, evidence suggests that inter-animal variations in the composition of extrusa samples are large and that there is a risk of confounding treatment and individual animal differences if such a method is used (Langlands 1967; Hodgson, 1969).

As previous experience of a given sward has been shown to affect the composition of the diet selected by an individual (Hodgson, 1969; Carulla, Lascano and Ward, 1991) the oesophageal fistulates used during this study were given the same opportunity to adapt to the different vegetation types as the core grazing animals and had equivalent experience of the layout of the experimental plots. Sampling was stimulated by starving the animals for a period prior to sample collection. The optimum length of time varied, with the goats and red deer requiring least encouragement and being penned for approximately one hour. In contrast the camelids were easily distracted from grazing and, unless they had spent a considerable time, at least three hours, without food, sampling was unsuccessful. However, evidence suggests that such periods of fasting do not affect the digestibility or chemical composition of the diet selected (Langlands 1967; Hodgson, 1969; Greenwood and Demment, 1988).

Following this period of food deprivation the fistula plugs were removed and polythene bags attached round the neck. The animals were then released and allowed to graze the appropriate sub-plot. If an animal regurgitated rumen contents into the bag the material was discarded. After forty-five minutes or as soon as an adequate quantity of extrusa had accumulated, whichever was sooner, the animals were returned to the handling pen, the bag removed and the plug replaced.

The extrusa samples collected were stored at -20°C prior to analysis. The saliva was left with the sample. This results in a degree of contamination with salivary salts and organic matter but has means that there is no loss of soluble plant compounds. The samples were divided and a representative subsample used to determine botanical composition while the was remainder freeze dried and milled through a 1 mm sieve in preparation for subsequent *in vitro* digestibility and n-alkane analyses. As with the herbage separations samples were freeze-dried rather than oven-dried to minimise loss of volatile compounds, especially water soluble carbohydrates and nitrogen.

Botanical composition of the extrusa was estimated by three operators taking replicate pinches of sample, suspending this in separate petri dishes of water and examining the suspension under a (x7) stereoscopic microscope (Olympus SZ, Tokyo) fitted with a gridded eyepiece. Any fragment of vegetation positioned under the intersection of lines on the grid was identified where possible as to taxon, morphological unit and state (green or dead). The petri dishes were examined systematically until 100 contacts had been recorded. As with the point quadrat method for establishing species composition of the vegetation available to the animal, this method is biased towards fragments of large leaves with their increased probability of lying beneath at least one intersection. However, this is unlikely to have unduly influenced the results in this case since extremes of leaf size were not found among the plant species encountered.

Statistical analysis was carried out on proportional data following an angular transformation. Firstly multiple regression was used to estimate the contribution of sources of variation to the observed inclusion rates of different vegetation categories in the diet. Following this a more detailed investigation was made of the principal sources of variation. A general feature of much of the data collected for the red deer and guanacos was a large number of missing values which resulted in the data being unbalanced. Thus different sources of variation were not balanced with respect to each other. To overcome this problem analysis has been carried out using Residual Maximum Likelihood (REML). This generated values for mean effects and standard errors of differences between means. T-tests were then used to determine significance of differences.

Diet selection was quantified by calculating electivity indices for each species of animal grazing each community using the modification by Jacob (1974) of Ivlev's Electivity Index:

$$D = (r - p)/(r + p - 2rp)$$

where r is the fraction of a given food type in the diet and p the fraction of the same food in the environment. D varied from -1 to 0 for negative selection and from 0 to +1 for positive selection.

Variation in the overall composition of the diets selected from each community by the three species of animal were investigated using Spearman's rank coefficient. In comparison with other rank coefficients this method gives weight to pairs of ranks that are further apart and is therefore more appropriate when there is less certainty about the reliability of close ranks.

During both experimental sessions in 1992 faeces samples were also collected from the oesophageal fistulates, stored at -20°C and prepared for n-alkane analysis as described in section 3.4.3 Intake. By comparing the overall alkane profile of the faeces of the core grazing animals with those of the oesophageal fistulates when grazing each of the communities the validity of assuming that oesophageal-fistulated animals consumed a similar diet to the intact animals could be assessed.

3.4.2 Diet digestibility

Digestibility, apart from being a nutritionally important measurement helps to integrate many of the separate aspects of selectivity such as consumption of green material in preference to dead herbage and leaf in preference to stem. However, the time and expense involved in collecting sufficient forage to feed animals for *in vivo* trials limits its application. Instead indirect methods of estimating *in vivo* digestibility have been developed.

It is possible to estimate diet digestibility using an appropriate marker assuming the marker is non absorbable, unaltered during passage through the animal, quantitatively recoverable; physically similar to or associated with the material it is to mark, does not affect the digestive process, and that feed and faeces are accurately sampled (Le Du and Penning, 1982). Satisfying these criteria is difficult. For example, although lignin has been widely used as an internal marker it can be digested to a certain (and variable) degree leading to the suggestion that this component should be used as a marker only when evidence exists that faecal recoveries approach 100 per cent (Fahey and Jung, 1983). More recently the use of n-alkanes as a marker to allow diet digestibility to be estimated has been proposed (Dove and Mayes, 1991). One of the main advantages of this approach is that digestibility can be determined simultaneously with herbage intake for individual intact grazing animals.

The more widely used alternative is an *in vitro* digestibility estimation (Tilley and Terry, 1963). However, in the case of *in vitro* determinations for grazing animals once again much is dependent on how representative the extrusa sample is of the diet consumed by a grazing animal. In addition ensalivation and mastication of herbage have been shown to affect *in vitro* organic matter digestibility values (Langlands, 1966).

Since this study offered a valuable opportunity to compare the results obtained from each of these methods, diet digestibility was calculated using both *in vitro* analysis of extrusa samples collected from oesophageal fistulates and n-alkane analysis of the faeces samples of the intact grazers following dosing with C_{36}.

In vitro digestibility of replicates of the freeze-dried and milled extrusa samples were carried out using the method of Tilley and Terry (1963) as modified by Alexander and McGowan (1966). Donor rumen liquor was obtained from rumen-fistulated sheep maintained on a hay diet. Included in the *in vitro* digestion procedure were *in vivo* standards for sheep derived from comparable vegetation types and fed undried at a level close to appetite (Armstrong, Common and Smith, 1986). Dry matter content and ash determinations were included in the analytical process, allowing results to be expressed on an organic matter basis. All analyses were done in duplicate and repeated if agreement was not satisfactory.

Diet digestibility was also estimated using the dosed n-alkane technique. Following daily dosing with C_{36} alkane faecal sampling and sample analysis (see 3.4.3 Intake) faecal output was estimated using the following equation:

$$\text{Faecal output (FO)} = (D_j/F_j) * 0.95$$

where D_j and F_j are the daily dose and faecal concentration of C_{36} respectively and a ninety-five percent recovery (0.95) of C_{36} in the faeces is assumed (R.W. Mayes, *pers. com*). Digestibility was then calculated using the equation below:

$$\text{Digestibility} = (\text{Intake - Faecal Output})/\text{Intake}$$

Again dry matter content and ash content determinations were carried out, and results expressed on an organic matter basis.

3.4.3. Intake

Similar considerations to those influencing which method of determining diet composition is most appropriate for a given situation will govern how intake is measured. Thus estimating food intake of wild herbivores generally relies on observations, preferably following standardisation of the recording system (Crawford and Whelan, 1973; Parker, Gillingham and Hanley, 1993).

In contrast, where domestic species of livestock are being studied more intensive methods of measuring intake can be employed without causing undue stress to the animal or altering its subsequent behaviour (Hatfield *et al.*, 1993). For example, herbage intake can be estimated from liveweight change during a period of grazing (Allden, 1962; Allden and Whittaker, 1970; Penning and Hooper, 1985) by harnessing the animals for faecal and urine collection, and correcting for additional weight losses weight losses estimated from fully harnessed animals not permitted to graze. The principal advantage of such this approach is the possibility of estimating intake over a relatively short period of time and/or when pasture conditions are changing rapidly.

However, total collection of faeces in the field is laborious and has many potential sources of error. As a result where an estimate of intake over longer periods is required faecal output is generally estimated from the dilution in faeces of a dosed indigestible marker. In the past chromium sesquioxide (Cr_2O_3) was most commonly used (Le Du and Penning 1982) either dosed twice daily or in ac continuous-release bolus (Parker *et al.*, 1990; Hatfield, Walker and Glimp, 1991). More recently attention has shifted to the potential of using dosed and herbage n-alkanes as markers for the determination of herbage intake (Mayes and Lamb, 1984; Mayes, Lamb and Colgrove, 1986; Ohajuruka and Palmquist, 1991) and Dove and Mayes (1991) review the potential advantages and disadvantages of these and other plant wax components to estimate intake.

Another approach to estimating forage intake has been the development of systems for detecting bolus swallowing (Forwood, Hulse and Ortbals, 1985; Forwood and Hulse, 1989; Forwood, da Silva and Paterson, 1991). However, the need for surgically-modified animals is likely to preclude the use of such equipment for large scale grazing trials, even if increased accuracy were established.

During this study herbage intake was estimated using the equation:

$$I = (F_i/F_j * D_j) / (H_i - (F_i/F_j) * H_j)$$

where I is daily herbage intake (kg OM/day), F_i and F_j are the faecal concentrations of specified odd-chain and even-chain alkanes; H_i and H_j the herbage concentrations of the same odd-chain and even-chain alkanes; and D_j the daily dose of a specified even-chain alkane.

During each experimental session herbage intake was estimated for the five core grazing animals of each species by daily dosing with pellets impregnated with C_{32} (dotriacontane) (and C_{36} (hexatriacontane) to estimate diet digestibility - see diet digestibility) using a sheep cobalt bolus dosing gun. Taking into account body weight along with predicted intake and diet digestibility values pellets weighing 1.0g (goats) and 1.6g (red deer and guanacos) were prepared (R.W. Mayes, *pers. com.*). The ratio

C_{32}:C_{33} was chosen as evidence indicates faecal recoveries of C_{32} and C_{33} alkanes are similar (Mayes, Lamb and Colgrove, 1986). Having established an equilibrium in the faecal concentration of dosed alkane during the run-in period and allowed forty-eight hours for the passage of vegetation eaten on the measurement plots faeces samples were collected daily from each animal for the last five days of the measurement week and stored at -20°C. These samples were then freeze-dried and milled in preparation for subsequent chemical analysis.

Subsequent chemical analysis was carried out following a modified version of the procedure outlined in Mayes, Lamb and Colgrove (1986). The principal difference was the omission of the unnecessary solvent extraction step prior to saponification of the crude extracts. Replicate weighed samples of extrusa or faeces (1.0g and 0.5g respectively) and internal standard (tetratriacontane, C34) were saponified in 1M alcoholic KOH. Following saponification the extracts were passed through silica gel columns to remove plant pigments and wax lipids such as the long-chain alcohols, leaving alkanes in the eluate. N-alkane levels were then determined using gas-liquid chromatography (PU4550, Pye Unicam Ltd, Cambridge) with two vials prepared and analysed per extraction. Peak areas of the n-alkanes were calculated using a Specra-Physics SP400 computing integrator (Hemel Hempstead, Herts.). Variations in the chromatography procedure were accounted for by regularly including standards and adjusting the sample results for differences between the estimated and known value of these standards.

3.4.4 Grazing pattern

A variety of methods are available to choose from when recording grazing time and ingestive behaviour of grazing animals. The most simple of these entails regular observations to collect data regarding location and activity. Such an approach is clearly time consuming and although labour requirements may by reduced by the use of time lapse photography or video cameras, results are dependent on prevalent environmental conditions and their effect on visibility. Accuracy of interpretation is also limited.

An alternative approach is to use equipment measuring head or jaw movements of individual animals. Comparatively simple mechanical devices such as Kienzle vibracorders mounted on the shoulder (Allden 1962) or head (Stobbs, 1970) have been used for some time. However, these and similar mechanisms such as the "grazing clock" (Jones and Cowper, 1975), although robust and simple, do not allow the identification of individual bites and so cannot provide information regarding total number of bites or bite rates.

In comparison recording systems consisting of a halter incorporating a transducer connected to a storage device can be used to produce analogue electrical signals of the jaw movements which can be subsequently replayed and analysed to give time spent grazing, ruminating and idling; and to count the jaw movements associated with these activities (Penning, 1983; Penning, Steel and Johnson, 1984; Matsui and Okubo, 1991; Matsui, 1994). As well as increased interpretation such devices have the advantage of offering data summarised on a minute by minute basis. The main disadvantage is equipment fragility.

Considering the increased risk of equipment damage associated with the species of animal under study reliability of data collection was considered to be of primary importance. Thus grazing time and grazing pattern were established using shoulder-mounted Kienzle vibracorders. These were fitted to the five core animals of each species during the last five days of the measurement period. To allow the animals to become accustomed to the harnesses these were introduced on the day prior to the measurement period. The clock mechanisms were then added on day three of the measurement week and the paper charts changed daily.

Central to the use of vibracorders is the assumption that if the animals head is moving up and down it is grazing. However, the animal may be involved in an activity unrelated to feeding. Equally it may be engaged in feeding behaviour, moving between patches and searching for food but not biting. To counteract this, during interpretation of the charts a minimum of five minutes uninterrupted trace was required to signal a change in behaviour.

Total grazing time for each day was calculated for each animal by summing the duration of the grazing bouts marked on the vibracorder chart. In addition the diurnal grazing pattern was established from each chart by recording at fifteen minute intervals whether or not a grazing bout was underway. This created a profile for each grazing animal for each day which could be used to assess the degree of consistency and synchronisation of grazing patterns. To determine whether grazing was more synchronised than would be expected by chance the kappa coefficient of agreement (K) was used as a coefficient of synchronisation (Rook and Penning 1991). This is defined as the ratio of the total proportion of synchronisation P(A) (corrected for chance synchronisation P(E)) to the maximum possible proportion of synchronisation, 1 (corrected for chance synchronisation) i.e.

$$K = (P(A) - P(E)) / (1-P(E))$$

Using vibracorders it was necessary to adopt an additional method of determining bite rate. This information was collected by visual observation. With such manual recording systems it is easier to record the time taken to make a specified number of bites rather than the total number of bites made in a fixed time interval. Therefore bite rates were calculated for the five core animals of each species during the measurement week by recording the time taken for an animal to make 100 bites. As jaw movements were judged to be difficult to observe accurately except at very close quarters head movements were recorded. These could normally be easily observed from a considerable distance and often even if an animal was partly obscured. Data was recorded while the animal was engaged in ingestive behaviour which would register as a grazing bout on the corresponding vibracorder chart, and included time spent by the animal moving between patches or searching for the next bite, i.e. time spent actively but unsuccessfully seeking acceptable mouthfuls of herbage to bite. Clearly such definitions are subjective but once established the same criteria for estimates of bite rate were used across species throughout the study.

3.5 STATISTICAL ANALYSIS

All statistical analyses were conducted using the GENSTAT statistical software program (version 5.2; Lawes Agricultural Trust, 1988).

3.6 SUMMARY

1. Goats, red deer and guanacos were studied on three contrasting vegetation types: a *Lolium perenne* dominated established sown sward; a *Nardus stricta* dominated indigenous grassland; and a *Calluna vulgaris* dominated dwarf-shrub community.

2. There was one spring and two summer experimental sessions at each site.

3. Species composition and canopy structure for each vegetation type were characterised using the point-quadrat technique and botanical separations.

4. Diet composition of the three species of animal on each vegetation type was established using oesophageal-fistulated animals. The extrusa samples collected also underwent *in vitro* analysis to determine diet digestibility.

5. Herbage intake was estimated using the n-alkane technique. The animals were dosed daily with C_{32} and grab samples collected. The animals were also dosed with C_{36} allowing diet digestibility to be estimated.

6. Total grazing time and grazing pattern were recorded using shoulder-mounted Keinzle vibracorders. Visual observations of bite rates were also made.

CHAPTER FOUR

VEGETATION PROFILES

4.1 INTRODUCTION

The availability of nutrients to a herbivore is a function not only of the chemical composition of the forage but also of the spatial distribution and abundance of the nutrients. Thus structure and heterogeneity of vegetation are factors which affect animal performance and require consideration in addition to measures of average mass and quality of forage available. Likewise, without a comprehensive profile of the vegetation available to an animal subsequent interpretation of diet composition results is limited. Therefore, a major component of this study was to quantify the vegetation available to the grazing animals.

The vegetation communities of temperate climates can be considered to fall into two broad categories; sown swards and indigenous communities; each of which offers different scope for manipulation of the quality and quantity of material selected and ingested by an animal. In comparison with indigenous swards sown pastures are generally characterised by being more homogeneous. These swards are typically dominated by monocultures of grass or grass/legume mixtures and are generally found on the more fertile soils. They tend to be highly productive both in terms of the quality and quantity of plant material. Consequently they are generally subjected to intensive management regimes and productivity is likely to be encouraged by applications of nitrogenous fertilisers.

Indigenous communities are generally composed of a wide range of plant species (Rodwell, 1992). However, despite the relative diversity in comparison with sown pastures there is likely to be consistency within communities in their overall composition as they are essentially composed of plants adapted to similar climatic, physiographic and edaphic factors. The distribution of the plant species within the community is less predictable as a result of localised variations in parameters including water content, aeration, concentration of key elements within the underlying soil, or microclimate

(Grime, Hodgson and Hunt, 1988). Conditions may also be influenced by the vegetation itself. Thus the dominant species within a community may modify environmental factors which in turn influence the number and distribution of additional species.

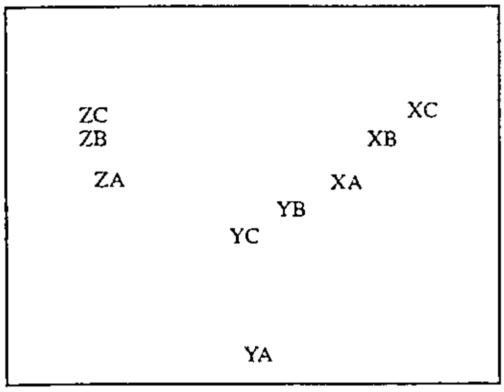
4.2 MATERIALS AND METHOD

The techniques which were used to establish species composition and canopy structure for each of the vegetation communities are described in Chapter Three along with details of the statistical analyses employed.

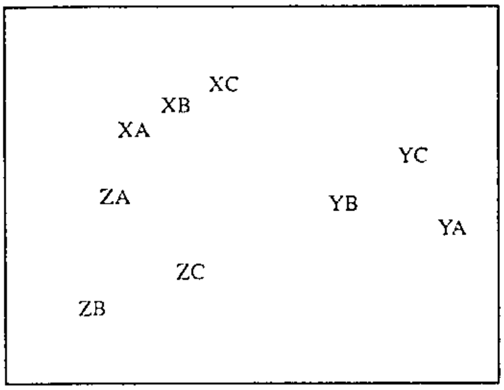
4.3 PRESENTATION OF RESULTS

Whilst the measurement area on each community had been split into three sub-plots to prevent interactions between the species of animal under study it was appreciated that significant inter-plot differences in the composition of the sward were possible, particularly on the heterogeneous indigenous vegetation. Thus it was necessary to test the validity of assuming the animals were exposed to the same foraging opportunities on each sub-plot. Using the point quadrat data inter-plot similarities were calculated and used to derive and plot principal co-ordinates. Distinct groupings according to session (summer 1991, spring 1992, summer 1992) could be identified (Figure 4.1). Thus the difference between a given sub-plot and the other two sub-plots from the corresponding session were less than the difference between the same sub-plot during the other two sessions. Likewise, multiple regression of the results of the botanical separations identified session as the main source of variation, with subplot having little effect. In light of these findings subsequent analysis was conducted across sub-plots on a community basis, unless otherwise stated.

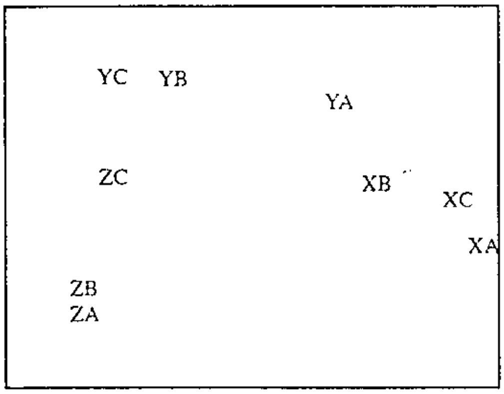
The results presented for each vegetation type follow a similar format with separate sections devoted to botanical composition, degree of clumping, canopy structure and biomass. By using this approach a profile of the overall sward is generated on a step-by-



Lolium



Nardus



Calluna

Key: X = summer 1991; Y = spring 1992; Z = summer 1992;
A = plot 1; B = plot 2; C = plot 3

Figure 4.1: Principal co-ordinate analysis of point-quadrat data.

step basis. Firstly the various components present in the sward are identified, secondly the horizontal distribution of these components is described, thirdly their vertical distribution within the canopy is established, and finally session and/or seasonal changes in the overall herbage biomass are considered.

To create a picture of the diversity of species of plant available to the grazing herbivore the composition of the measurement areas on each community during each experimental session have been depicted in a series of graphs generated using the point quadrat data. A pie chart featuring plant categories present within the sward and identifiable within the diet summarises the overall composition of the vegetation. In each case the dominant species, defined as the species which occurs with greatest frequency in the most important stratum of the community, has been 'drawn out' for emphasis. Where the plant category is composed of a number of species, e.g. broad-leaved grasses, a stack-graph has been produced to illustrate the contribution of each. Thus the contribution of each individual species of plant identified can be gauged.

To characterise the sward in more detail, in terms of vegetation categories identifiable within the diet, the point quadrat data has been tabulated according to plant type, morphological unit (leaf, stem, flower) and state (green, dead). These categories take into consideration ecological and morphological similarities between plants; and the accuracy of identification of fragments in extrusa samples collected by oesophageal fistulated animals. By considering only the first hit of each point quadrat needle and assigning these to similar categories the sward surface of each community on each occasion has also been characterised. These sets of proportional data were used for subsequent comparison with the proportions of the corresponding categories in the diet and are plotted in the graphs depicting diet selection on each community in Chapters Five, Six and Seven.

The computer program (I. Finlayson, *pers. com.*) available to summarise point quadrat data provided percentage specific frequency information for a given area without at any stage taking into account variability between quadrats. Thus standard errors would only be available across subplots; i.e. based on only three observations per category. For this reason the results of the botanical separations, which give at least eighteen observations per category, have been used as the basis for statistical analysis of variance between sessions and season in the contribution of each category to the composition of the sward. The biomass separations were also analysed to obtain an estimate of the *in vitro* digestibility of each vegetation category during each experimental session.

Calculation of the Green's index (GI) for each species (see Chapter Three) gave an assessment of the degree of clumping of the different species encountered.

The point quadrat data has also been used to create a series of graphs depicting the distribution of plant categories within horizons in the sward. The first series of graphs for each sward type groups the plant species present into the broadest categories of monocotyledons and dicotyledons. Subsequent graphs give particular emphasis to graminoid species from the Lolium and Nardus swards and *Calluna vulgaris* from the dwarf-shrub community, and illustrate the effect of season and sward horizon on the distribution of morphological units of these.

During the botanical separations unattached dead vegetation was considered to be the equivalent of the point quadrat category 'litter'. The bulk of this material, over seventy per cent for the Nardus community and eighty per cent for the Lolium pasture and Calluna community, was located at the base of the sward, i.e. within the first two height bands on the sward profile graphs. This transient element within the sward has been excluded from subsequent analyses. To simplify the sward profile graphs, moss has also been excluded. Although the amount of moss recorded on the Lolium pasture was negligible, this plant category made a significant contribution to the indigenous communities although it was rarely encountered in the diet (see Chapters Five, Six and Seven). Once again the majority of hits were recorded at the base of the sward: over eighty and ninety per cent for Nardus and Calluna communities respectively.

Finally, from the weights of samples cut within quadrats herbage biomass (kgDM/m^2) was calculated and compared. However, as it was impossible to account for variations in moisture content due to climatic conditions, no comparison is made between sessions in the percentage dry matter of the herbage available.

Nomenclature of vascular plants follows Clapham, Tutin and Moore (1987).

RESULTS

4.4 THE LOLIUM SWARD

4.4.1 Species composition

The overall species composition of the Lolium swards as determined using the point quadrat technique is tabulated in Table 4.1. In addition to the dominant graminoid species nine further species of broad-leaved grass were encountered. All were native and perennial with the exception of *Poa annua* which is an annual or short-lived perennial. Nine species of dicotyledonous plants were recorded, including white clover. Of these eight species other than clover, *Ranunculus repens, Cerastium fontanum, Rumex obtusifolium, Bellis perennis* and *Plantago major* are perennial. The remaining three are annuals. All are native and common in improved swards or where cultivation has taken place.

The contribution of each species of plant encountered to the diet composition categories (stack-graphs) and the proportion of the total sward accounted for by these categories (pie-chart) are illustrated in Figures 4.2a, 4.2b and 4.2c for summer 1991, spring 1992

Dietary category	**Family**	**Genus**	**Common name**
broad-leaved grasses	Gramineae	*Agrostis canina*	brown bent-grass
		Agrostis capillaris	common bent-grass
		Deschampsia cespitosa	tufted hair-grass
		Dactylis glomerata	cock's foot
		Holcus mollis	creeping soft grass
		Phleum pratense	timothy
		Poa annua	annual meadow-grass
		Poa pratensis	smooth meadow-grass
		Poa trivialis	rough meadow-grass
clover	Papilionaceae	*Trilfolium repens*	white clover
other dicotyledonous plants	Caryophyllaceae	*Cerastium fontanum*	mouse-ear chickweed
		Stellaria media	chickweed
	Compositae	*Bellis perennis*	daisy
	Cruciferae	*Capsella bursa-pastoris*	shepherd's purse
	Plantagineae	*Plantago major*	great plantain
	Polygonaceae	*Polygonum aviculare*	common knotgrass
		Rumex obtusifolius	broad-leaved dock
	Ranunculaceae	*Ranunculus repens*	creeping buttercup

Table 4.1: Plant species encountered on the Lolium community in addition to *Lolium perenne.*

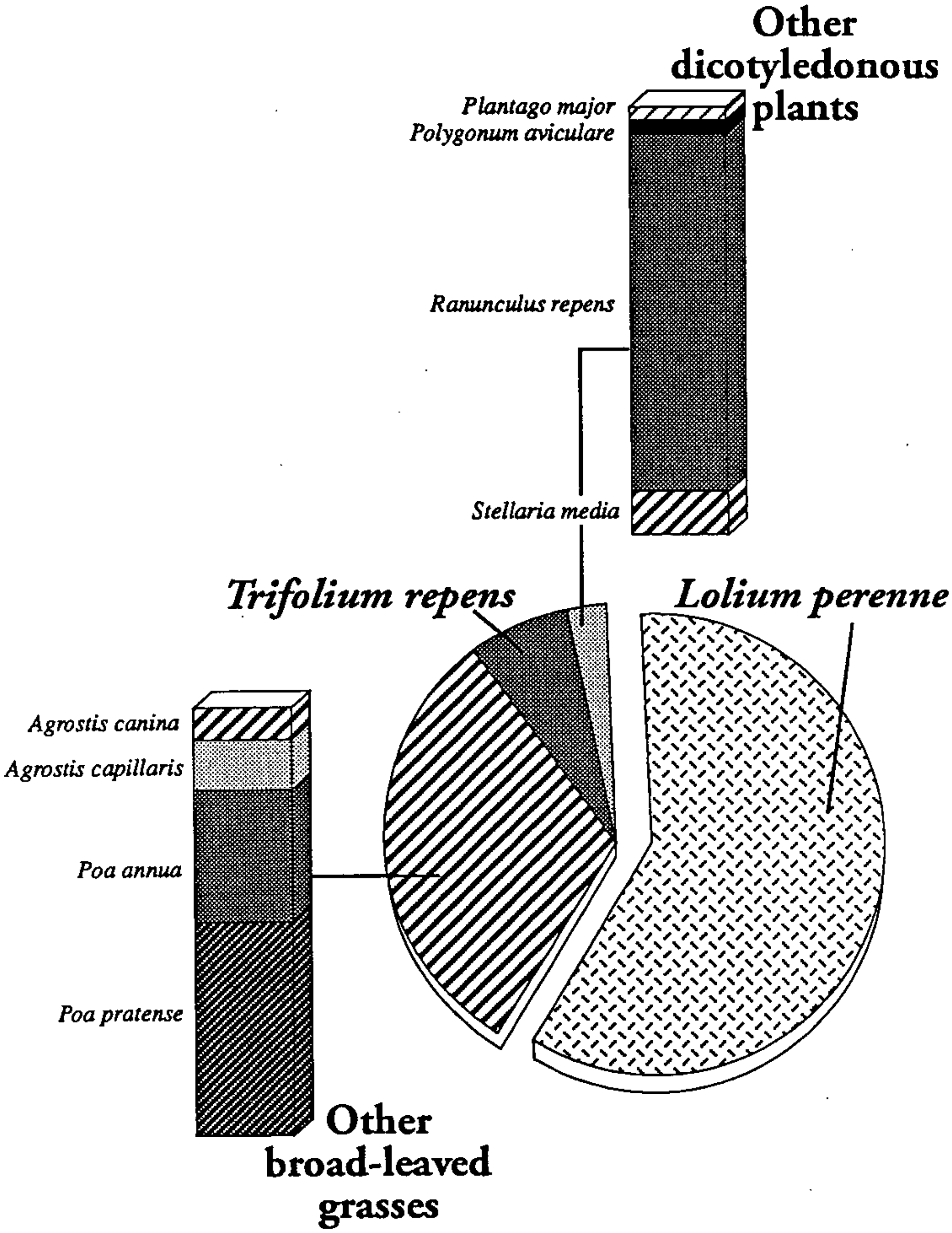


Figure 4.2a: Contribution of individual plant species to the overall composition of the *Lolium* sward in summer 1991

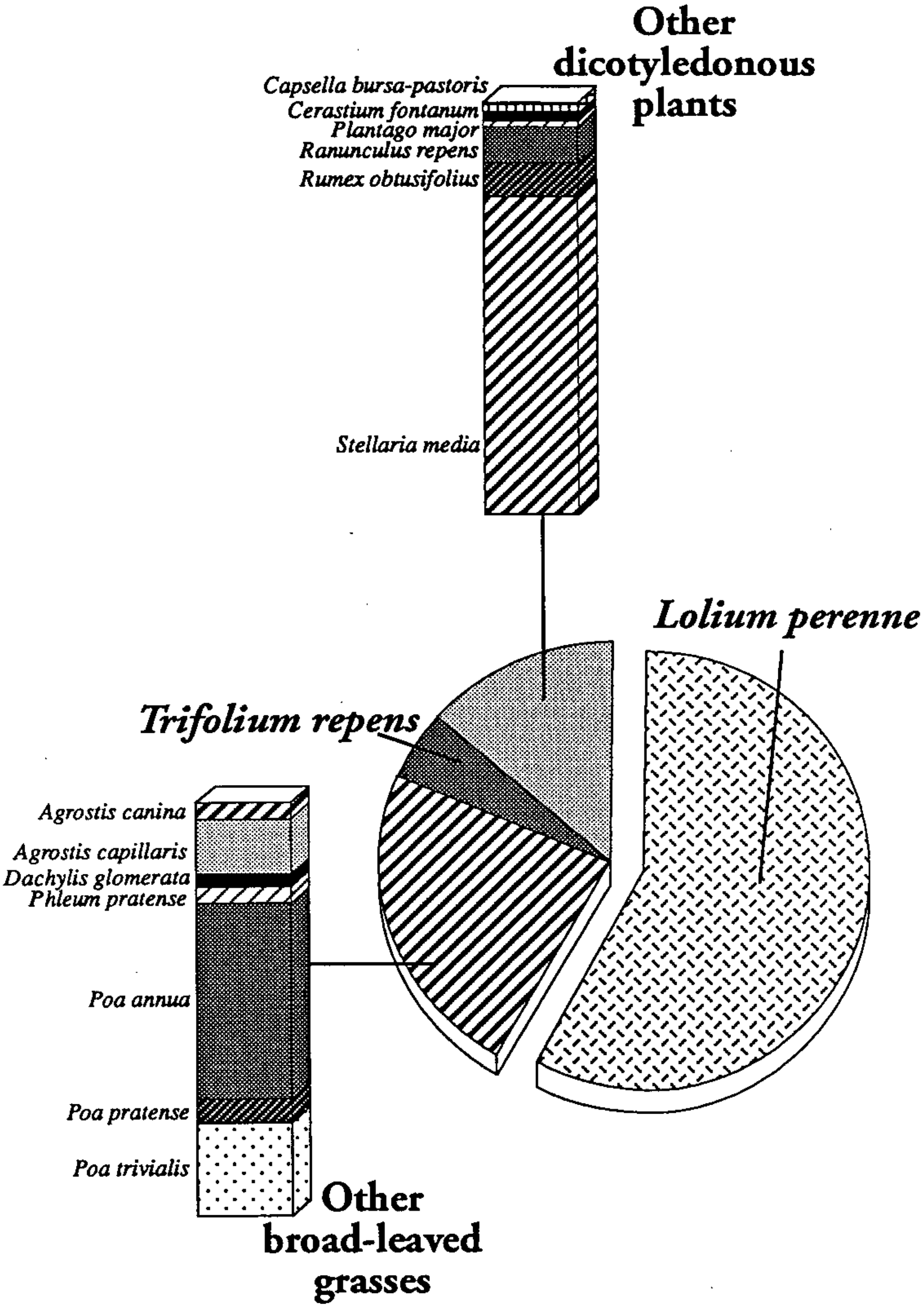


Figure 4.2b: Contribution of individual plant species to the overall composition of the *Lolium* sward in spring 1992

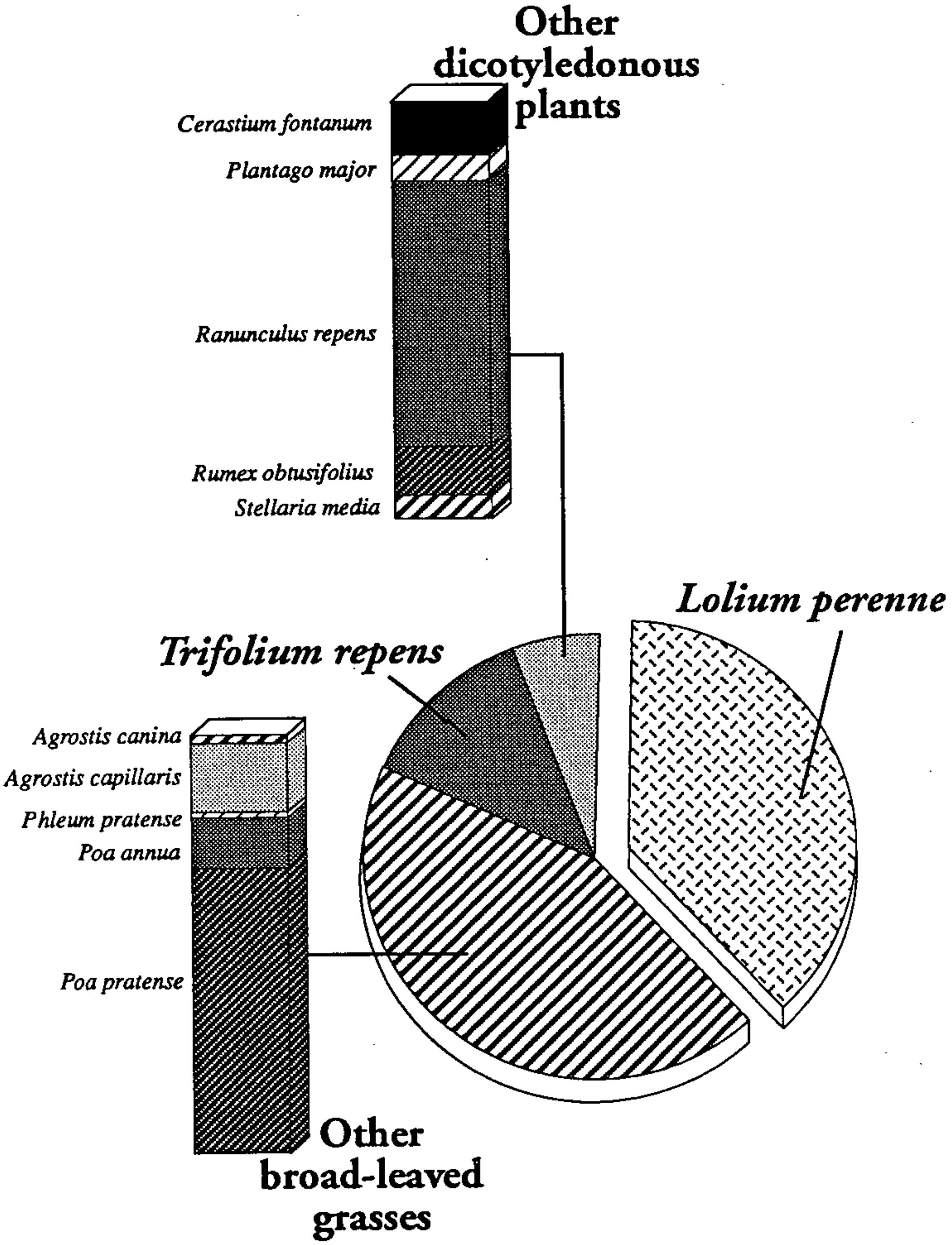


Figure 4.2c: Contribution of individual plant species to the overall composition of the *Lolium* sward in summer 1992

and summer 1992 respectively.

In general over eighty per cent of the hits were broad-leaved grasses, and although there was a relative reduction in the proportion of *Lolium perenne* encountered during the third experimental session this species remains dominant irrespective of season.

There was an increase in the proportion of dicotyledonous plants in the sward when the results for the experimental periods in 1992 are compared with those from 1991. During the spring session this can be attributed to the 'other dicotyledonous plant' category accounting for an increased portion of the sward (see section 4.4.2 for statistical analysis) while the clover content remained similar to that recorded in 1991. By the summer session a decrease in 'other dicotyledons' resulted in the ratio of this category to clover being close to that in summer 1991 while the overall contribution of dicotyledonous plants remained similar to that in spring 1992.

4.4.2 Effect of session on sward composition

The effect of session and season on the composition of the sward in terms of categories based on plant species, morphological units and state (live/dead) was determined using the botanical separations data. Table 4.2 gives a summary of statistically significant differences.

There was a statistically significant reduction in the proportion of green lamina of broad-leaved grasses in summer 1992 in comparison with the previous two sessions, while the sward in spring 1991 had significantly less dead lamina than either summer session. The proportion of vegetative stem was lower in summer 1991 in comparison with spring or summer 1992. There was a significant reduction in the flowerstem content of the samples collected in summer 1992 when compared with spring 1992. Likewise summer 1992 had a reduced proportion of flower and seedhead in comparison with both summer

Vegetation category			**Summer 1991 v. Spring 1992**	**Summer 1991 v. Summer 1992**	**Spring 1992 v. Summer 1992**	
broad-leaved grasses	leaf	green	*	*	ns	$\phi\psi$
		dead	ns	*	**	
grass vegetative stem			ns	***	ns	$\phi\psi$
grass flowerstem			**	*	ns	$\phi\psi$
grass seed/flowerhead			**	ns	***	
Trifolium repens	leaf	green	ns	ns	ns	ψ
		dead	**	*	ns	$\phi\psi$
	petiole		ns	*	***	ψ
other dicots	leaf	green	***	*	ns	$\phi\psi$
		dead	ns	ns	ns	
	stem		ns	ns	ns	
	flower		ns	**	**	

ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$

ϕ = plot effect

ψ = plot x session interaction

Table 5.2: Summary of statistical analysis comparing the diets selected by the goats from the Lolium sward during each experimental session

sessions.

The proportions of live and dead leaf of *Trifolium repens* were unaffected by season. However, an increase in the occurrence of clover petiole was recorded in summer 1992 in comparison with both summer 1991 and spring 1992. Other dicotyledonous species were more prevalent in the spring session than either of the summer sessions.

Estimates of the *in vitro* digestibility of these vegetation categories during each experimental session are tabulated in Table 4.3.

4.4.3 Green's index

The Green's index value for each species present is listed in Table 4.4. There was little clumping of the species of broad-leaved grass recorded on the *Lolium perenne* dominated pasture. Likewise, *Trifolium repens* was dispersed across the measurement area. Although the degree of clumping of additional dicotyledonous species varied, even the highest index values corresponded to a relatively dispersed distribution.

4.4.4. Sward profile

The first series of graphs (Figure 4.3) shows the distribution of monocotyledonous and dicotyledonous plants within the sward for the different experimental sessions. While dicotyledonous plants were found in each height band up to 15-17.5 cm, grasses were recorded at up to 33-35.5 cm. Thus on each occasion there was a section at the top of the sward consisting only of grasses. The most striking difference between the three profiles was the reduction in sward height in the summer of 1992 compared with the two previous experimental sessions. This was associated with the base of the sward being altered through a marked increase in the proportion of monocotyledonous material occurring in the 0 - 2.5cm and 3 - 5.5cm strata. There was also an increased contribution of dicotyledonous plants to the sward in 1992, with again the main change

Vegetation category		Summer 1991	Spring 1992	Summer 1992
broad-leaved grasses	leaf green	0.784 ± 0.0097	0.806 ± 0.0060	0.777 ± 0.0017
	dead	0.487 ± 0.0097	0.581	0.450 ± 0.0143
grass vegetative stem		0.780 ± 0.0058	0.751 ± 0.0164	0.742 ± 0.0115
grass flowerstem		0.422	0.744 ± 0.0067	0.410
grass seed/flowerhead		-	0.751	-
Trifolium repens	leaf green	0.800	0.815	0.797
other dicots		0.734	0.755 ± 0.0039	0.754

mean ± s.e.m. across sub-plots

no s.e.m. = value for bulked sample from entire measurement area

\- = insufficient sample

Table 4.3: *In vitro* digestibility values for vegetation categories from the Lolium sward during each experimental session.

Genus	**Summer 1991**	**Spring 1992**	**Summer 1992**
Agrostis canina	0.1037	0.0535	0.1939
Agrostis tenuis	0.1412	0.0526	0.0276
Dactylis glomerata	-	0.0441	-
Lolium perenne	0.0012	0.0009	0.0026
Phleum pratense	-	-	0.1446
Poa annua	0.0528	0.0431	0.1068
Poa pratensis	0.0092	0.0469	0.0036
Poa tenuis	-	0.0280	-
Trilfolium repens	0.0078	0.0280	0.0181
Cerastium fontanum	-	-	0.1032
Stellaria media	-	0.0041	0.1594
Plantago major	-	0.0428	0.3070
Rumex obtusifolius	-	0.1453	0.1777
Ranunculus repens	0.0646	0.0163	0.0120

Values range between 0 - 1: 0 = random and 1 = maximum clumping

Table 4.4: Green's index values for plant species encountered on the Lolium sward.

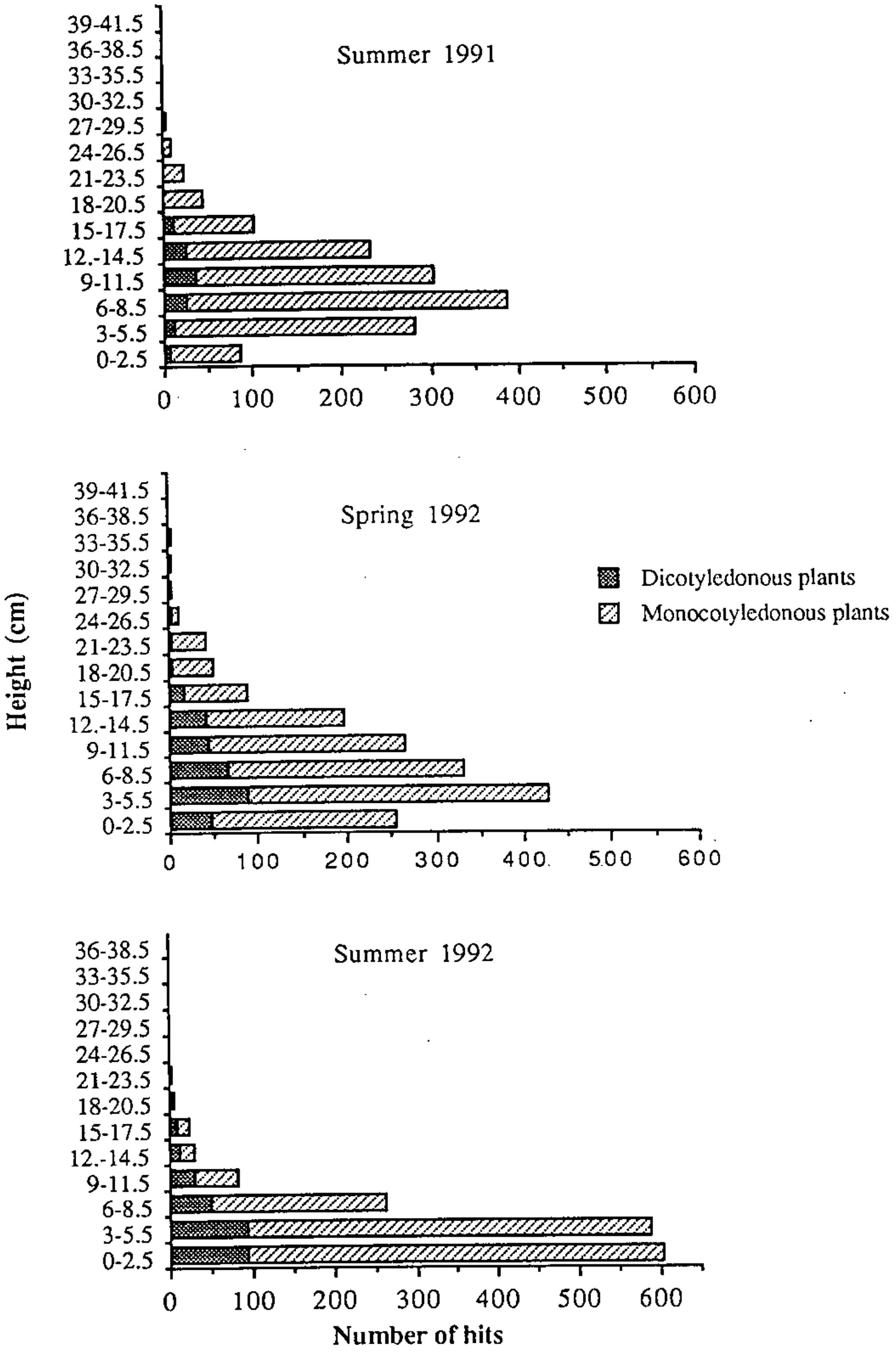


Figure 4.3: Distribution of monocotyledonous and dicotyledonous plants within the Lolium sward canopy during each experimental session.

in overall profile occurring at the base of the sward.

The second group of graphs (Figure 4.4) plots the profile of the morphological units of the broad-leaved grasses. Again the relative reduction in sward height in summer 1992 and the associated effects on the base of the sward are apparent. In contrast to summer 1991 when the densest strata was 6.0 - 8.5cm, the greatest density of material was found from 0 - 2.5cm. However, common features can also be identified within the three swards. For example, on all occasions leaf was distributed throughout the sward. Similarly, for all three swards vegetative stem was located within the lower half of the sward while flowerstem occurred at all heights, irrespective of season.

The third set of graphs (Figure 4.5) concentrates on the distribution of green and dead leaf within the sward. Like vegetative stem dead leaf was located within the lower horizons of the sward and was found also in the strata where the green leaf was most dense (summer 1991 6.0 - 8.5cm: spring 1992 3.0 - 3.5: summer 1992 3.0 - 3.5). Once again the difference between the profiles for summer 1992 and the other profiles is worthy of comment because of the increased proportion of dead material in summer 1992.

To summarise the composition and canopy structure of the sward the proportions of the total sward and sward surface accounted for by the equivalent of dietary categories are listed in Table 4.5. Green lamina of broad-leaved grasses accounted for a greater proportion of the sward surface than the total sward. In contrast, the percentage of dead lamina and vegetative stem at the sward surface were consistently lower than in the total sward. A similar trend was found for the different proportions of *Trifolium repens* with the proportion of green leaf higher at the sward surface but those of dead leaf and petiole lower. The proportion of hits identified as dicotyledonous plants other than *Trifolium repens* was similar at the surface to that recorded for the sward as a whole.

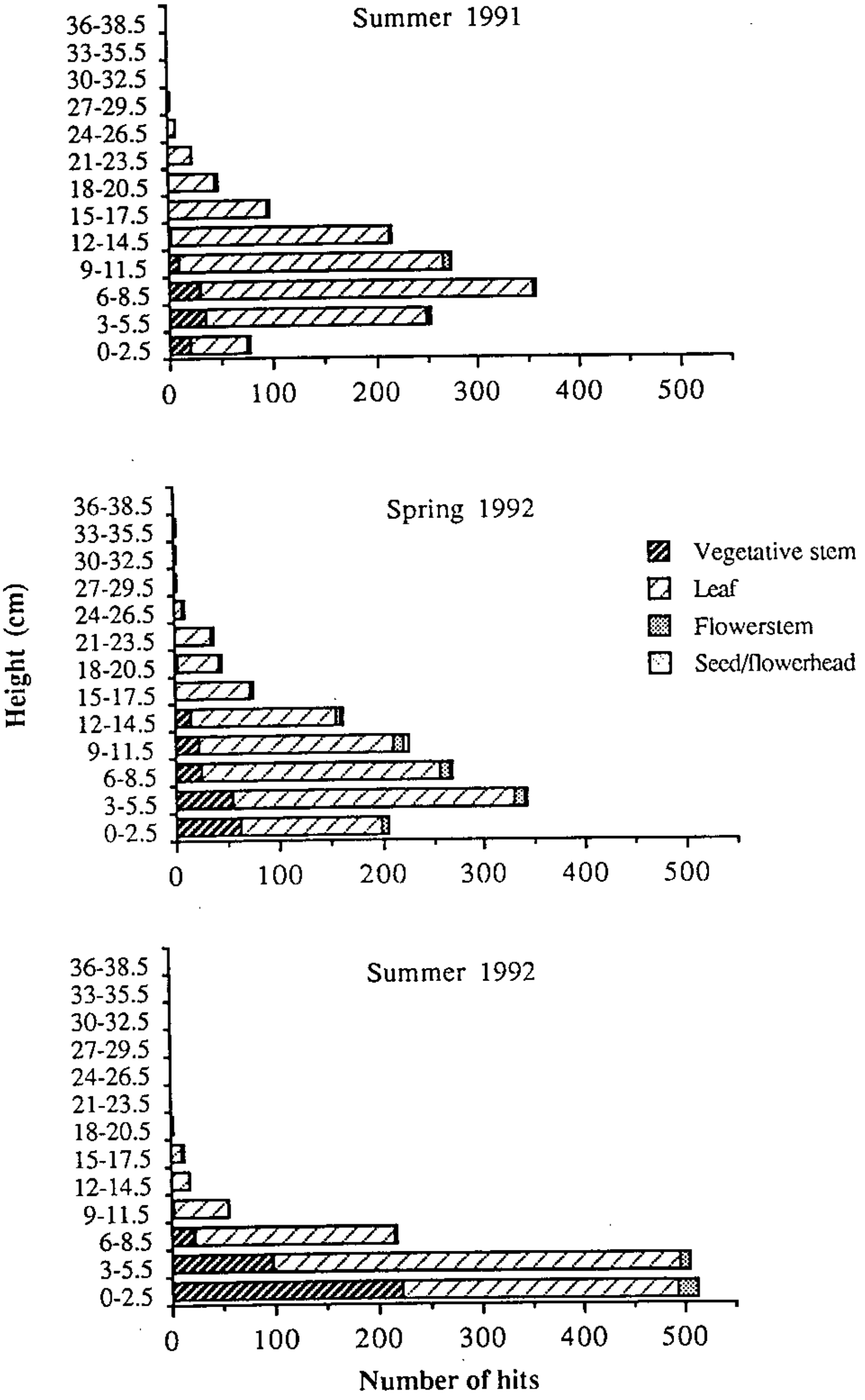


Figure 4.4: Distribution of morphological units of broad-leaved grasses within the Lolium sward canopy during each experimental session.

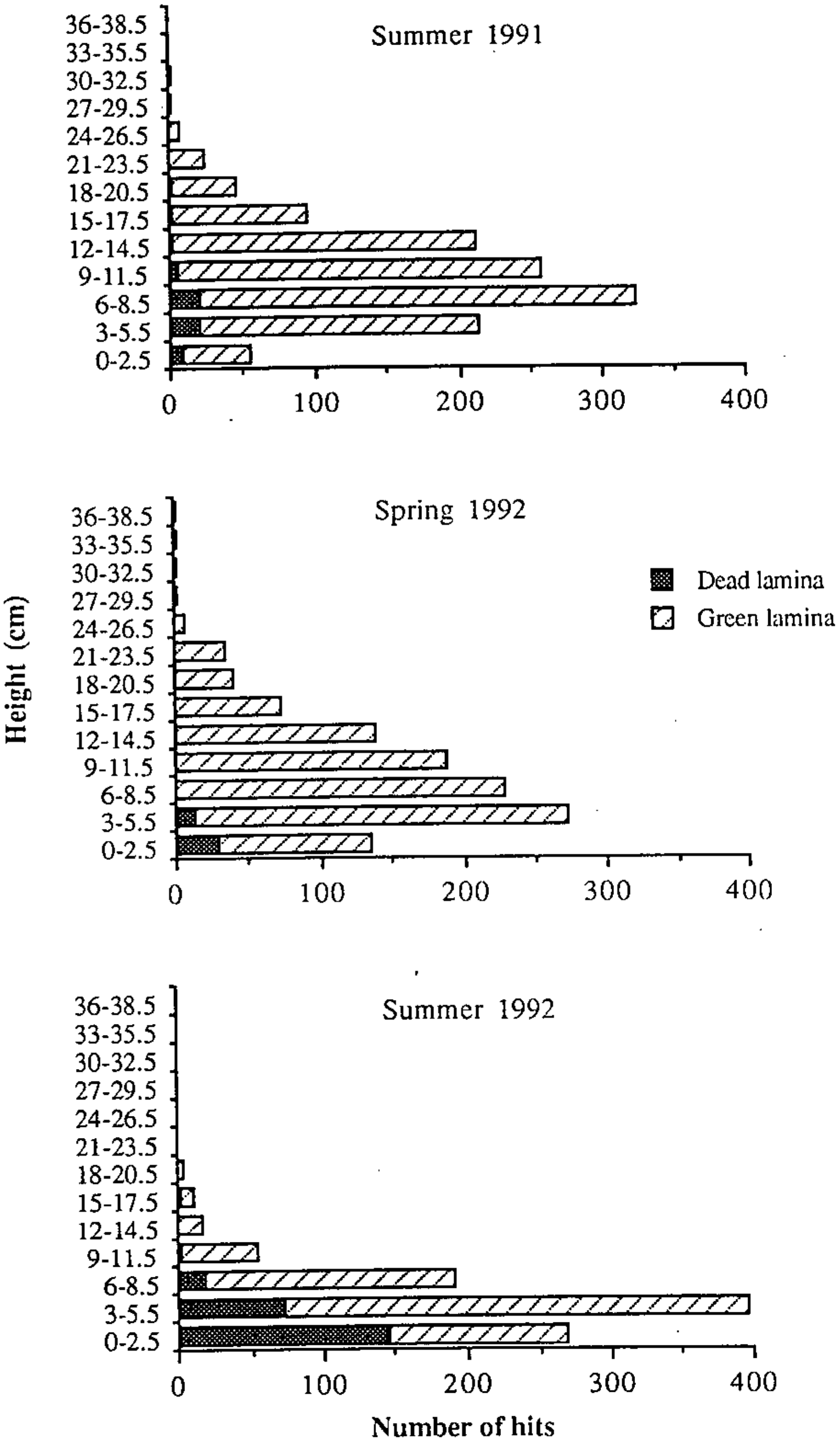


Figure 4.5: Distribution of green and dead lamina of broad-leaved grasses within the Lolium sward canopy during each experimental session.

			Summer 1991		**Spring 1992**		**Summer 1992**	
Vegetation category			Total	Surface	Total	Surface	Total	Surface
broad-leaved grasses	leaf	green	79.7	82.9	60.7	76.2	43.0	65.3
		dead	4.1	2.4	7.4	0	14.6	2.8
grass vegetative stem			6.6	1.0	10.8	1.7	21.2	2.5
grass flowerstem			1.3	1.4	2.9	1.7	2.2	2.5
grass seed/flowerhead			0.4	1.0	0.8	2.9	0.1	0
Trifolium repens	leaf	green	4.1	6.7	4.0	8.3	10.4	17.3
		dead	0.3	0	0.6	0	0.5	0
	petiole		0.9	1.0	0.1	0	1.2	0
	flower		0	0	0	0	0.1	0
other dicots	leaf	green	2.0	3.2	7.7	8.2	4.8	8.3
		dead	0.2	0	1.0	0	0.4	0
	stem		0.3	0.3	4.5	0.5	1.4	1.3
	flower		0	0	0.1	0.5	0	0

Table 4.5: Proportions of total Lolium sward and sward surface only accounted for by categories equivalent to those used during analysis of diet composition.

4.4.5 Biomass

The mean herbage biomass and herbage dry matter percentage for each experimental period are given in Table 4.6. There was a significantly higher herbage biomass for the Lolium pasture in summer 1992 compared with the two previous experimental sessions (compared with summer 1991 $p < 0.001$; compared with spring 1992 $p < 0.001$).

4.5 THE NARDUS COMMUNITY

4.5.1 Species composition

The species composition of the Nardus measurement area is listed in Table 4.7. In addition to the dominant tussock-grass, two further species of fine-leaved grass and nine species of broad-leaved grass were encountered. With the exception of *Poa annua,* which can be an annual or short-lived perennial, all are native perennials. Also perennial are the various members of the Cyperaceae and Juncaceae families grouped together and labelled 'other monocotyledonous plants'. As identification of individual species of *Carex* and *Luzula* would have been prohibitively time-consuming classification was based on genera only. Six species of perennial dicotyledonous plant were also encountered.

The contribution of each of these species (stack-graphs) to the overall composition of the sward (pie-charts) is depicted in Figures 4.6a, 4.6b and 4.6c for summer 1991, spring 1992 and summer 1992 respectively. *Nardus stricta,* as the dominant species within the community, accounted for approximately forty per cent of the hits on each occasion. The remaining species were found in the inter-tussock areas.

The proportions of broad- and fine-leaved grasses within the sward were similar. The contribution of the various species encountered to the broad-leaved grass category was similar for all three experimental sessions, with *Agrostis* spp. the most prevalent. In contrast, when the stack-graphs for the fine-leaved grasses are compared, there is an

Session	Herbage biomass (gDM/m2)		Dry matter (%)	
	mean	s.e.m.	mean	s.e.m.
Summer 1991	379.8	25.81	23.9	1.32
Spring 1992	395.9	23.96	16.6	0.47
Summer 1992	589.2	36.64	27.7	1.11

Table 4.6: Herbage biomass (gDM/m2) and herbage dry matter percentage of the Lolium sward during each experimental session.

Dietary category	Family	Genus	Common name
broad-leaved grasses	Gramineae	*Agrostis canina*	brown bent-grass
		Agrostis capillaris	common bent-grass
		Anthoxanthum odoratum	scented vernal grass
		Deschampsia cespitosa	tufted hair-grass
		Dactylis glomerata	cock's foot
		Holcus mollis	creeping soft-grass
		Molinia caerulea	purple moor-grass
		Poa annua	annual meadow-grass
		Poa pratensis	smoth meadow-grass
fine-leaved grasses		*Deschampsia flexuosa*	wavy hair-grass
		Festuca ovina	sheep's fescue
other monocotyledonous plants	Cyperaceae	*Carex*	sedges
		Eriophorum angustifolium	common cotton-grass
		Trichophorum cespitosum	deer grass
	Juncaceae	*Juncus squarrosus*	heath rush
		Luzula	wood rush
dicotyledonous plants	Ericaceae	*Vaccinium myrtillus*	blaeberry
		Vaccinium vitis-idaea	cowberry
	Papilionaceae	*Trifolium repens*	white clover
	Polygonaceae	*Rumex obtusifolius*	dock
	Rosaceae	*Potentilla erecta*	common tormentil
	Rubiaceae	*Galium saxatile*	heath bed-straw

Table 4.7: Plant species encountered on the Nardus community in addition to *Nardus stricta.*

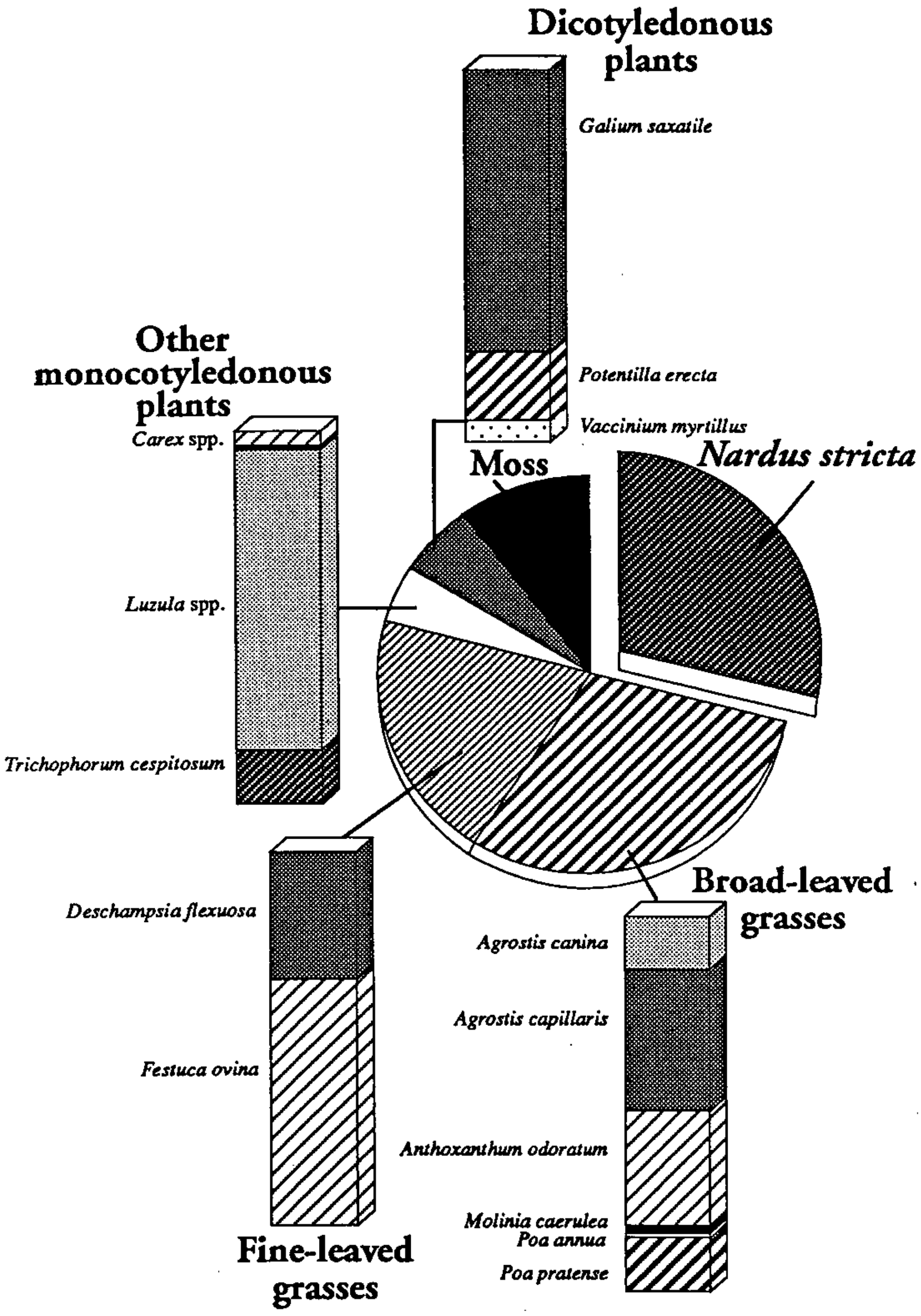


Figure 4.6a: Contribution of individual plant species to the overall composition of the *Nardus* community in summer 1991

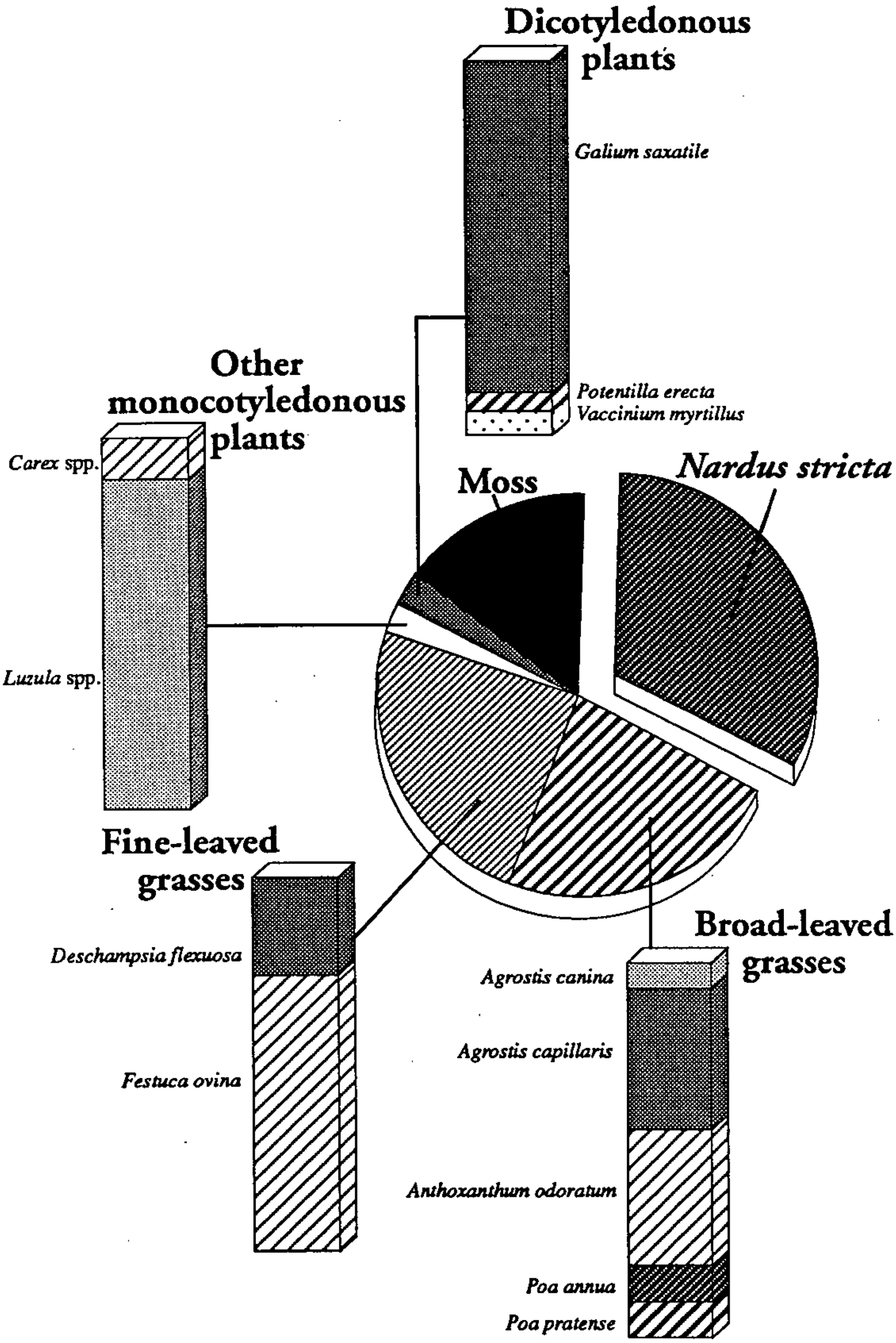


Figure 4.6b: Contribution of individual plant species to the overall composition of the *Nardus* community in spring 1992

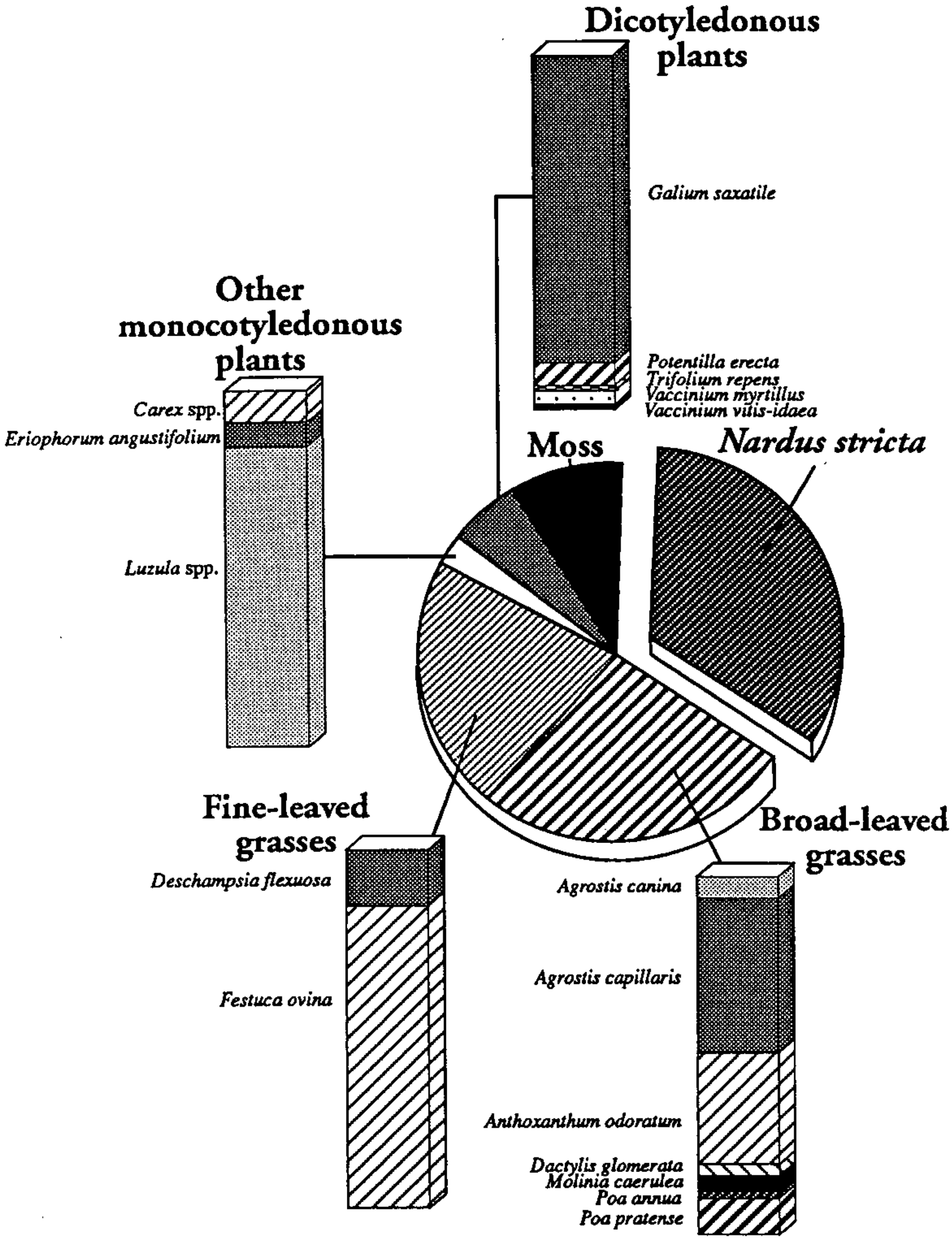


Figure 4.6c: Contribution of individual plant species to the overall composition of the *Nardus* community in summer 1992

apparent trend towards an increase in *Festuca ovina* at the expense of *Deschampsia flexuosa* over the three experimental sessions.

Moss was a consistent feature of the sward. In comparison 'other monocotyledonous plants' and 'dicotyledonous plants' made only minor contributions. Species of *Luzula* are clearly the most influential of the non-grass monocotyledons accounting for over eighty per cent of the hits within the category, with *Carex* spp. the other consistent contributors to this portion of the sward. *Galium saxatile* was the dicotyledon most frequently encountered within the swards. *Potentilla erecta* and *Vaccinium myrtillus* were also found to be present during the three experimental sessions, while *Trifolium repens* and *Vaccinium vitis-idaea* made a minor contribution to the summer 1992 sward.

4.5.2 Effect of session on composition of inter-tussock areas

The effect of session and season on the composition of the inter-tussock areas in terms of categories based on plant species, morphological unit and state (live/dead) was investigated using the botanical separations data (as outlined in Chapter Three samples had been taken from the inter-tussock areas only). A summary of statistically significant differences is given in Table 4.8.

When considering the contribution of plant groups consisting of graminoid plant parts a number of statistically significant differences between sessions were recorded. For example, a significantly higher proportion of dead *Nardus stricta* leaf was recorded in spring 1992 in comparison with summer 1992. Green lamina of broad-leaved grasses significantly was higher in the summer 1992 experimental period compared with the previous spring experimental period. Likewise, the incidence of dead lamina of broad-leaved grasses was significantly higher in summer 1992 than in the two summer sessions. The occurrence of dead lamina of fine-leaved grasses was significantly lower during summer 1991. During the third experimental period there were significantly higher

Vegetation category			**Summer 1991 v. Spring 1992**	**Summer 1991 v. Summer 1992**	**Spring 1992 v. Summer 1992**	
Nardus	leaf	green	ns	ns	ns	
		dead	ns	ns	**	
broad-leaved	leaf	green	ns	ns	**	ϕ
grasses		dead	ns	***	**	
fine-leaved	leaf	green	ns	ns	ns	
grasses		dead	**	**	ns	
grass vegetative stem			*	***	ns	
grass flowerstem			ns	**	*	ϕ
grass seed/flowerhead			ns	ns	ns	ϕ
Carex	all	green	ns	ns	ns	
		dead	ns	ns	ns	
	leaf	green	ns	ns	ns	
		dead	ns	ns	ns	ψ
other monocots.	all	green	ns	ns	ns	
		dead	ns	ns	ns	
Galium	all	green	ns	ns	ns	ϕ
		dead	ns	ns	ns	ϕψ
Vaccinium	all	green	ns	ns	ns	
		dead	ns	ns	ns	
Potentilla	all	green	ns	ns	ns	
		dead	ns	ns	ns	
moss			ns	ns	ns	

ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$
ϕ = plot effect
ψ = plot x session interaction

Table 4.8: Summary of statistically significant differences between sessions in the contributions of vegetation categories to the overall composition of the Nardus community.

levels of grass flowerstem recorded but no corresponding differences were found between sessions in the proportion of grass seed/flowerheads. The session with the lowest stem content, summer 1991, has a significantly higher proportion of vegetative stem in comparison with either session in 1992.

No statistically significant differences were found between the proportions of the dicotyledonous species in the community. Likewise, the proportion of *Carex* spp. and *Luzula* spp. was similar during all three sessions. As such components, particularly those located in the lower strata of the sward, would be more susceptible to significant changes in sward structure and associated changes in competition for resources they may be used to gauge consistency between sessions. The stability of these species indicates that although the proportions of live and dead morphological units of the grass categories may have fluctuated, the overall structure and character of the sward was maintained.

The biomass separations were also analysed to obtain an estimate of the *in vitro* digestibility of each vegetation category during each experimental session (Table 4.9).

4.5.3 Green's index

The GI value for each species is listed in Table 4.10. The low values of GI calculated for *Nardus stricta* indicate that it was evenly distributed across the measurement area. There was also little clumping of the more common of the broad-leaved species of grasses, including *Agrostis canina, Agrostis capillaris* and *Anthoxanthum odoratum*. The two species of *Poa* were more clumped in comparison. The species of broad-leaved grass with a high GI value, such as *Holcus mollis* and *Dactylis glomerata,* were not located during all three experimental sessions. The two species of fine-leaved grasses other than *Nardus stricta* showed little clumping.

The degree of clumping of *Carex* spp. varied but was relatively constant for *Luzula* spp..

Vegetation category			Summer 1991	Spring 1992	Summer 1992
Nardus stricta	leaf	green	0.582 ± 0.0102	0.662	0.580
		dead	0.403	0.378 ± 0.0077	-
broad-leaved grasses	leaf	green	0.679 ± 0.0128	0.777 ± 0.0012	0.682 ± 0.0072
		dead	0.431 ± 0.0230	0.438	0.424 ± 0.0051
fine-leaved grasses	leaf	green	0.637 ± 0.0155	0.700 ± 0.0055	0.619 ± 0.0058
		dead	0.412	0.423 ± 0.0024	0.391 ± 0.0053
grass vegetative stem			0.487 ± 0.0215	0.496 ± 0.0172	0.561 ± 0.0084
grass flowerstem			0.516	0.466	0.516 ± 0.0156
Luzula	leaf	green	0.560	-	-
dicots.	all	green	0.598	0.611	0.623
moss		green	0.326 ± 0.0092	0.377 ± 0.0267	0.333 ± 0.0025
		dead	0.273	-	-

mean ± s.e.m. across sub-plots

no s.e.m. = value for bulked sample from entire measurement area

\- = insufficient sample

Table 4.9: *In vitro* digestibility values for vegetation categories from the Nardus community during each experimental session.

Species	Summer 1991	Spring 1992	Summer 1992
Agrostis canina	0.0043	0.0210	0.0110
Agrostis tenuis	0.0154	0.0087	0.0151
Anthoxanthum odoratum	0.0038	0.0063	0.0052
Deschampsia cespirosa	-	-	0.8661
Dactylis glomerata	-	-	
Holcus mollis	0.9231	-	0.5625
Molinia caerulea	0.6251	-	0.2355
Poa annua	0.9580	0.0388	-
Poa pratensis	0.0193	0.0831	0.0491
Deschampsia flexuosa	0.0061	0.0056	0.0114
Festuca ovina	0.0053	0.0033	0.0045
Nardus stricta	0.0035	0.0032	0.0022
Carex spp.	0.0067	0.0485	0.1670
Eriophorum angustifolium	-	-	0.3104
Trichophorum cespitosum	0.5104	-	-
Juncus squarrosus	-	-	-
Luzula spp.	0.0358	0.0220	0.0223
Potentilla erecta	0.0268		0.0253
Galium saxatile	0.0101	0.0070	0.0067
moss	0.0024	0.0013	0.0009

Values range between 0 - 1: 0 = random and 1 = maximum clumping

Table 4.10: Green's index values for plant species encountered on the Nardus community.

Of the dicotyledonous plant species there was a higher degree of clumping of *Vaccinium myrtillus* than either *Potentilla erecta* or *Galium saxatile*. Moss and litter were distributed across the entire measurement area.

4.5.4 Sward profile

A similar approach to that used for the Lolium sward was implemented to create an overall picture of the structure of the Nardus grassland. Again the first series of graphs (Figure 4.7) differentiates between monocotyledonous and dicotyledonous plants occurring at different height bands. Once more dicotyledonous plants did not feature in the upper height bands of the sward. This was also the case for non-grass monocotyledonous plants, which have been plotted separately from the graminoid species reflecting their dietary importance. Apart from a reduction in overall sward height in spring 1992 the profiles for all three experimental sessions are similar, with the sward consistently at its most dense at 3.0 - 3.5cm irrespective of season.

With animals expected to graze from the species-rich inter-tussock areas *Nardus stricta* has been plotted separately from the other grass species. The graphs which depict the morphological structure of the *Nardus stricta* tussocks (Figure 4.8) indicate that in addition to a reduction in the overall sward height being recorded in spring relative to the summer experimental sessions, a substantial seasonal change in composition occurred. There was a large increase in the incidence of dead leaf and a corresponding decease in green leaf at all height-bands. A second notable difference is the absence of grass flowerstem and inflorescence categories in spring.

Despite a similar reduction in overall sward height the seasonal variation which was evident in the composition of the profiles of the *Nardus stricta* tussocks was not found when the distribution of the morphological units of the inter-tussock grass species is considered (Figure 4.9). Vegetative stem was concentrated at the base of the sward

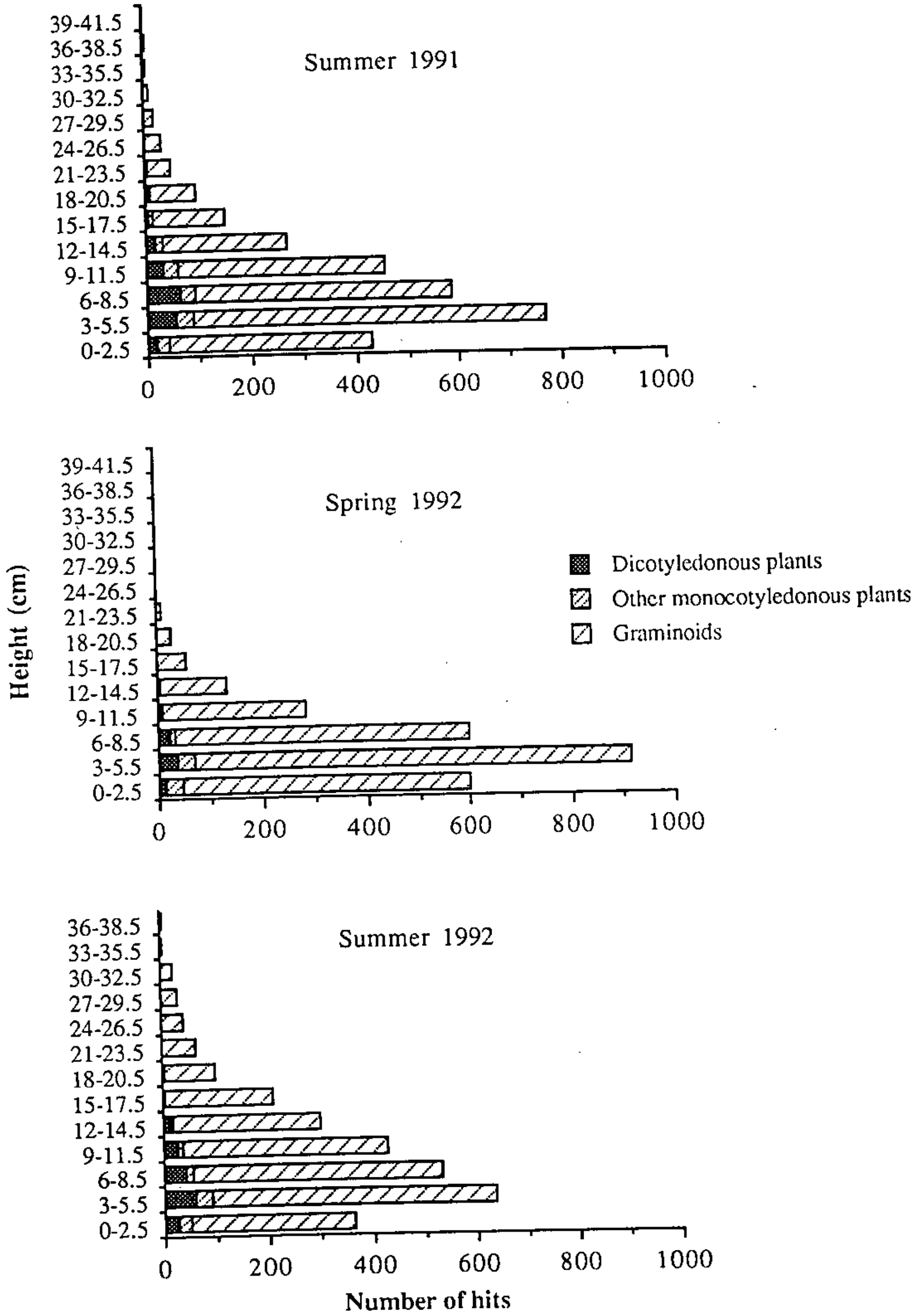


Figure 4.7: Distribution of graminoids, other monocotyledonous plants and dicotyledonous plants within the Nardus community canopy during each experimental session.

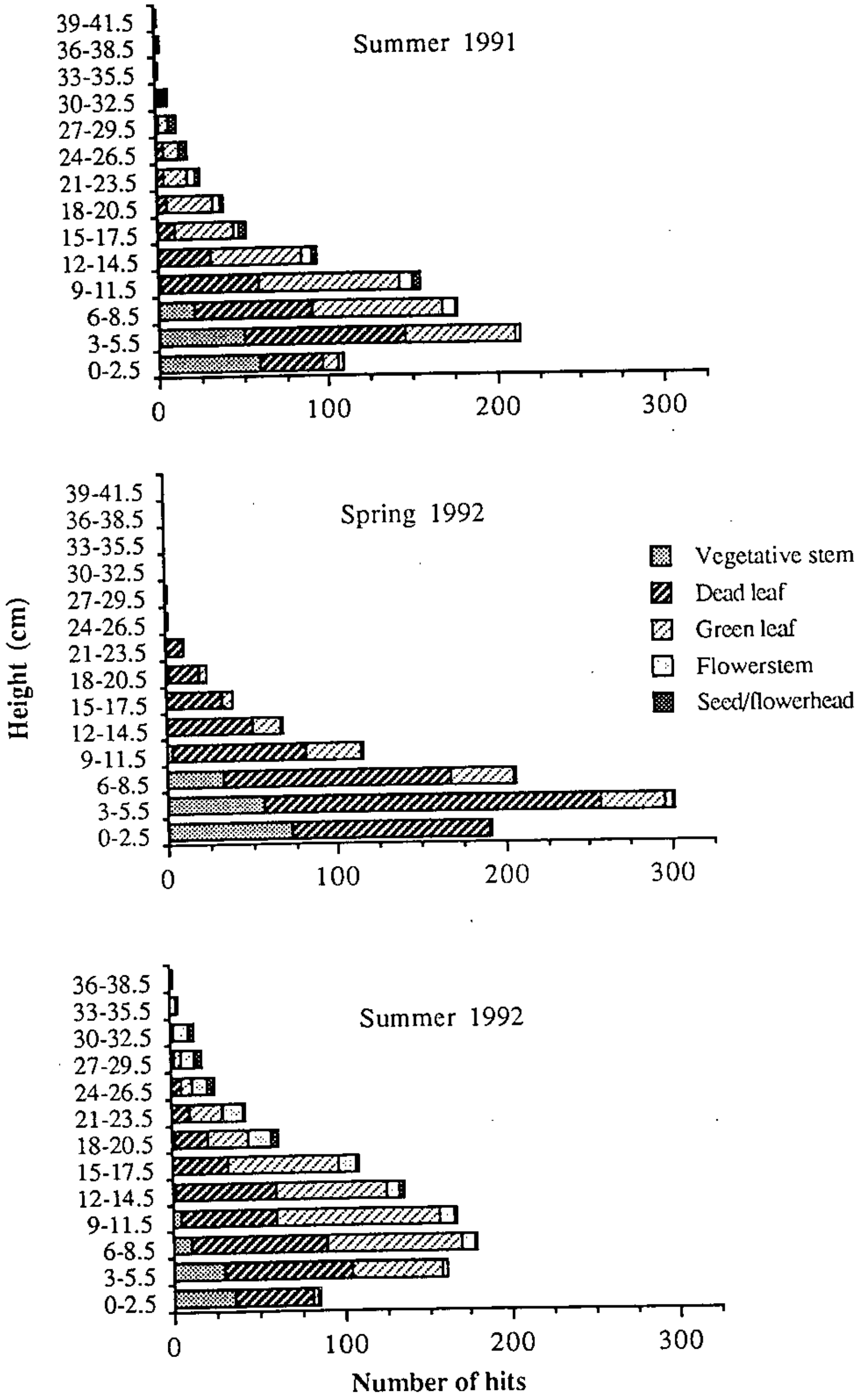


Figure 4.8: Distribution of morphological units of *Nardus stricta* during each experimental session.

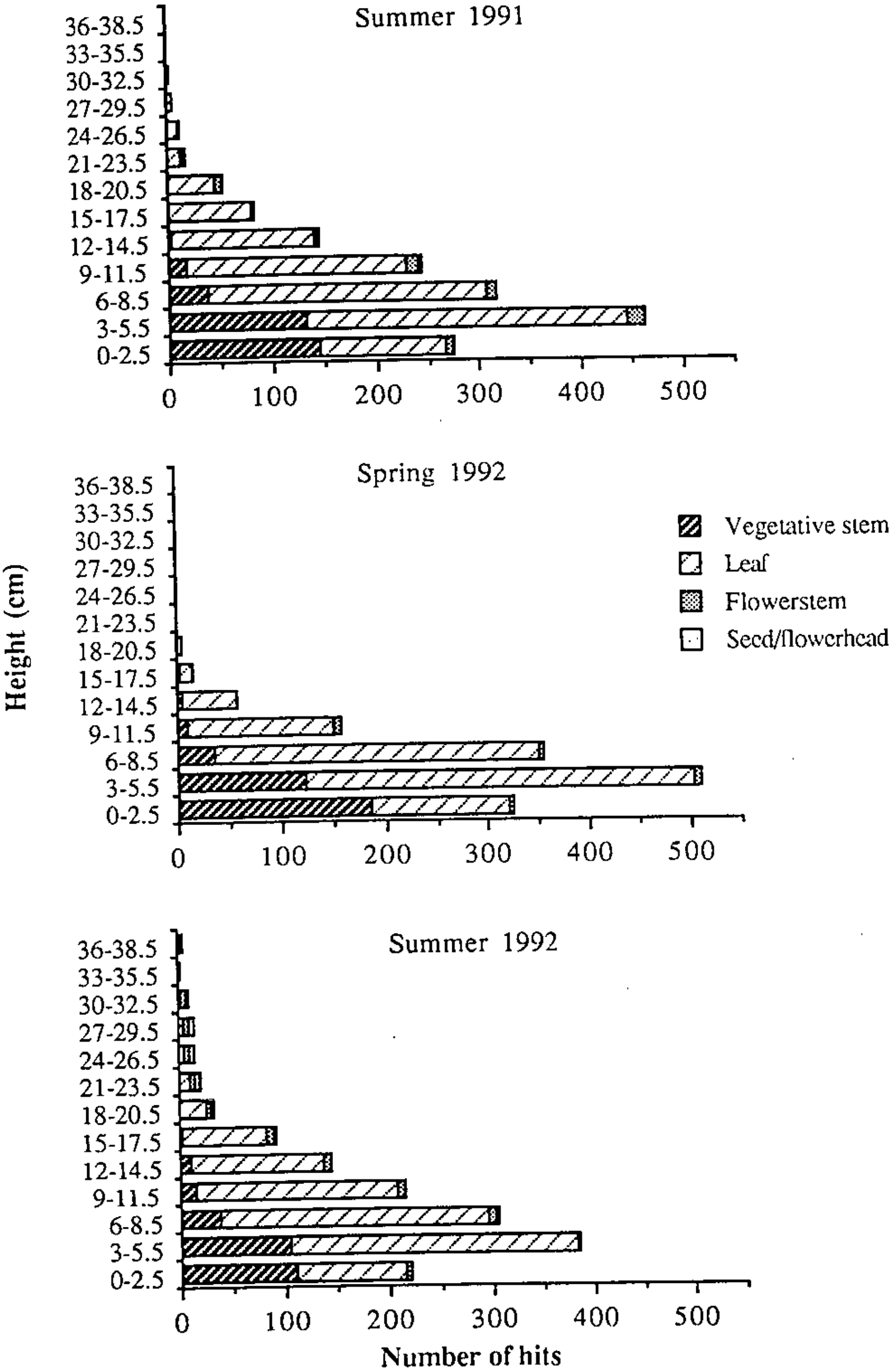


Figure 4.9: Distribution of morphological units of inter-tussock grasses within the Nardus community canopy during each experimental session.

whereas the number of flowerstem hits was constant for all height-bands and correspondingly accounts for an increasing proportion as the sward height increases.

Due to the dietary importance of the inter-tussock grass species the distribution of live and dead lamina of broad and fine-leaved grasses has been plotted separately (Figure 4.10). Once again the reduction in overall sward height was evident, but in contrast to the *Nardus stricta* tussocks there was not a dramatic change in the proportions of green and dead leaf. However, as the frequency of hits and distribution of dead leaf did not alter between sessions, the taller swards of the summer sessions were characterised by having their upper half consisting only of green leaf whereas in spring dead leaf was encountered at all height bands.

The composition and canopy structure of the sward the proportions of the total sward and sward surface accounted for by the equivalent of dietary categories are summarised in Table 4.11. It is this data which has been plotted for comparison with the results on dietary composition reported in Chapters Five, Six and Seven. While slight variations in the proportions of categories of grass leaf can be identified the most striking difference between the sward as a whole and the surface only was the reduction in grass vegetative stem. Also noteworthy is the increase in seed/flowerhead at the surface during the summer session. A number of minor components, such as dead *Vaccinium myrtillus* and *Potentilla erecta* were never encountered at the sward surface.

4.5.5 Biomass

The mean herbage biomass and herbage dry matter percentage for each session are given in Table 4.12. There was a statistically significant decrease in the herbage biomass of the inter-tussock areas of the *Nardus* community between the spring and summer experimental sessions (compared with summer 1991 $p < 001$; compared with summer 1992 $p < 0.01$).

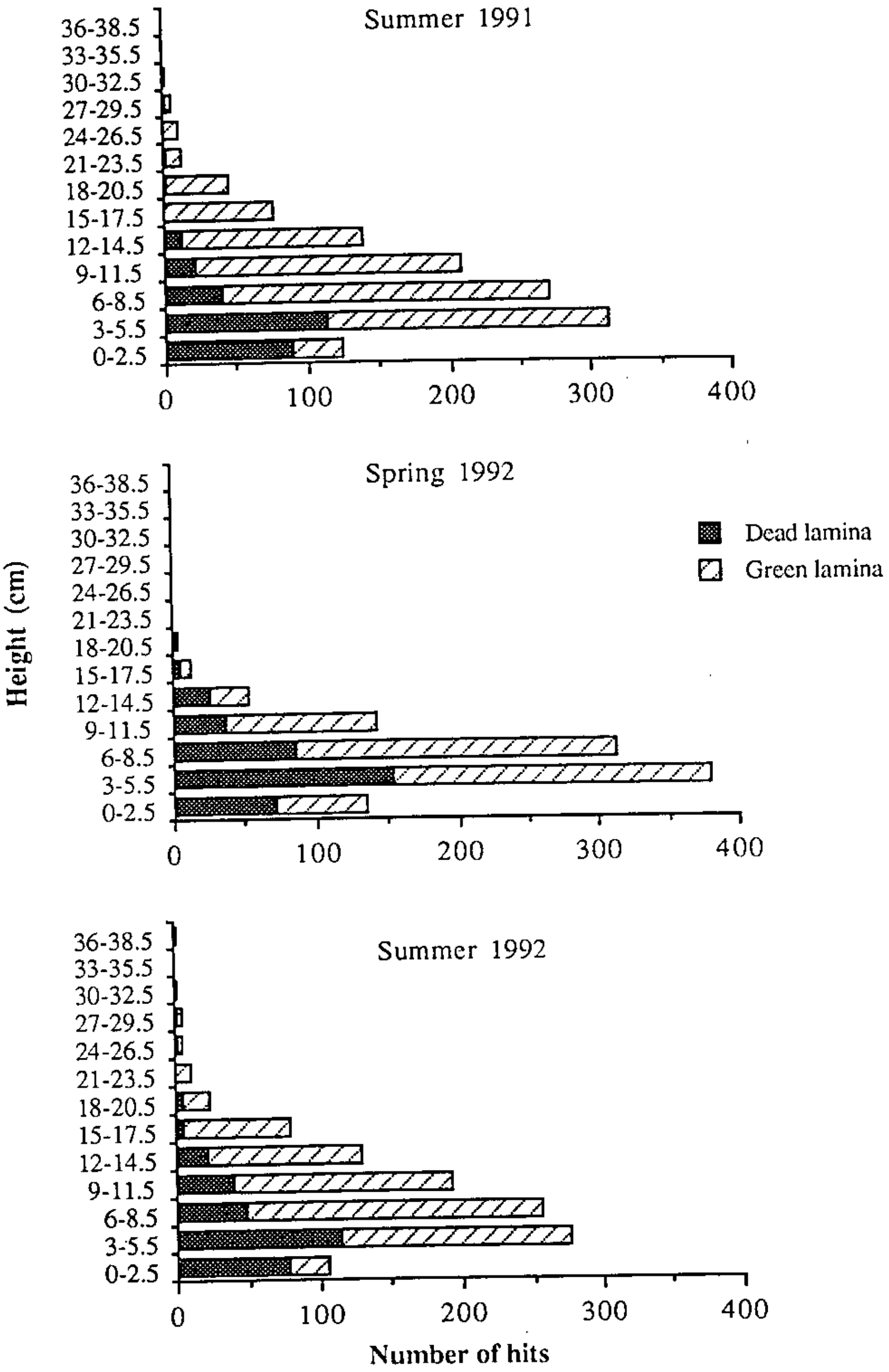


Figure 4.10: Distribution of green and dead lamina of inter-tussock grasses within the Nardus community canopy during each experimental session.

			Summer 1991		**Spring 1992**		**Summer 1992**	
Vegetation category			Total	Surface	Total	Surface	Total	Surface
Nardus	leaf	green	12.0	23.1	4.7	8.5	14.0	21.7
		dead	10.1	5.3	21.6	29.1	12.9	10.0
broad-leaved grasses	leaf	green	20.0	35.8	11.9	21.0	15.7	21.7
		dead	4.6	0.8	5.3	5.4	4.3	1.7
Festuca	leaf	green	5.4	4.5	7.1	10.4	8.1	9.6
		dead	3.6	0	6.5	3.5	5.9	1.4
Deschampsia	leaf	green	3.7	2.0	2.9	6.2	1.7	2.8
		dead	0.7	0.3	0.9	0.6	0.3	0
grass vegetative stem			14.7	1.2	17.4	2.8	12.1	0.4
grass flowerstem			2.4	7.7	1.1	1.5	5.4	17.7
grass seed/flowerhead			2.3	9.5	0.2	0.4	1.9	8.4
Carex		green	0.2	0	0.1	0.2	0.3	0.6
		dead	0	0	0.2	0.2	0	0
	leaf	green	2.3	2.6	1.1	1.3	1.2	1.0
		dead	1.4	0	1.2	0.7	1.2	0.2
Galium	all	green	4.6	2.2	2.4	1.7	5.2	1.3
		dead	0.2	0.3	0	0	0.1	0
Potentilla	all	green	1.1	1.8	0.1	0.2	0.4	0.6
Vaccinium	all	green	0.3	0.3	0.1	0	0.2	0
		dead	0.1	0	0	0	0.1	0
other dicots			0	0.2	0	0	0.1	0
moss			9.7	2.0	15.3	6.2	8.8	0.6

Table 4.11: Proportions of total Nardus sward and sward surface only accounted for by categories equivalent to those used during analysis of diet composition.

Session	Herbage biomass (gDM/m2)		Dry matter (%)	
	mean	s.e.m.	mean	s.e.m.
Summer 1991	1049.4	67.66	36.9	1.00
Spring 1992	686.1	57.19	47.8	1.17
Summer 1992	966.7	54.47	38.9	0.88

Table 4.12: Herbage biomass (gDM/m2) and herbage dry matter percentage of the Nardus community during each experimental session.

4.6 THE CALLUNA COMMUNITY

4.6.1 Species composition

The species composition during each of the experimental sessions as determined using the point quadrat is tabulated in Table 4.13. In addition to *Calluna vulgaris* two further species of evergreen dwarf shrub, *Empetrum nigrum* and *Erica tetralix*, were encountered. Two species of *Vaccinium* , *V. myrtillus* and *V. vitis-idaea*, were identified which differ in being deciduous and evergreen respectively. The other two species of dicotyledonous plant encountered were both native perennial herbs. Only three graminoids were recorded. Two of these, *Deschampsia flexuosa* and *Festuca ovina*, were fine-leaved grasses and the other broad-leaved. Three non-grass monocotyledonous genera, *Eriophorum, Juncus* and *Luzula*, were also identified.

The contribution of each of these species (stack-graphs) to the overall composition of the community (pie-chart) is depicted in Figures 4.11a, 4.11b and 4.11c for summer 1991, spring 1992 and summer 1992 respectively. On each occasion the dominant species, *Calluna vulgaris*, accounted for at least sixty per cent of the total hits recorded. In comparison the other two heaths made little contribution. Of these consistently more *Empetrum nigrum* than *Erica tetralix* was encountered. 'Other dicotyledonous plants' and 'monocotyledonous plants' were recorded more frequently than 'other heaths'. *Vaccinium myrtillus* was consistently the principal contributor to the 'other dicotyledonous plant' portion of the sward. Of the monocotyledonous species the frequency of hits of *Festuca ovina* was highest in summer 1991 but *Deschampsia flexuosa* accounted for the majority of hits in spring and summer 1992. However, on each occasion it was the moss category which ranked as accounting for the second largest proportion of the sward after *Calluna vulgaris*.

4.6.2 Effect of session on sward composition

The effect of session and season on the composition of the sward was determined using

Dietary category	**Family**	**Genus**	**Common name**
other heaths	Ericaceae	*Empetrum nigrum*	crowberry
		Erica tetralix	cross-leaved heath
other dicotyledonous plants	Ericaceae	*Vaccinium myrtillus*	blaeberry
		Vaccinium vitis-idaea	cowberry
	Rosaceae	*Potentilla erecta*	common tormentil
	Rubiaceae	*Galium saxatile*	heath bed-straw
monocotyledonous plants	Gramineae	*Agrostis canina*	brown bent-grass
		Deschampsia flexuosa	wavy hair-grass
		Festuca ovina	sheep's fescue
	Cyperacaea	*Eriophorum angustifolium*	common cotton-grass
	Juncaceae	*Juncus squarrosus*	heath rush
		Luzula spp.	wood rush

Table 4.13: Plant species encountered on the Calluna community in addition to *Calluna vulgaris*.

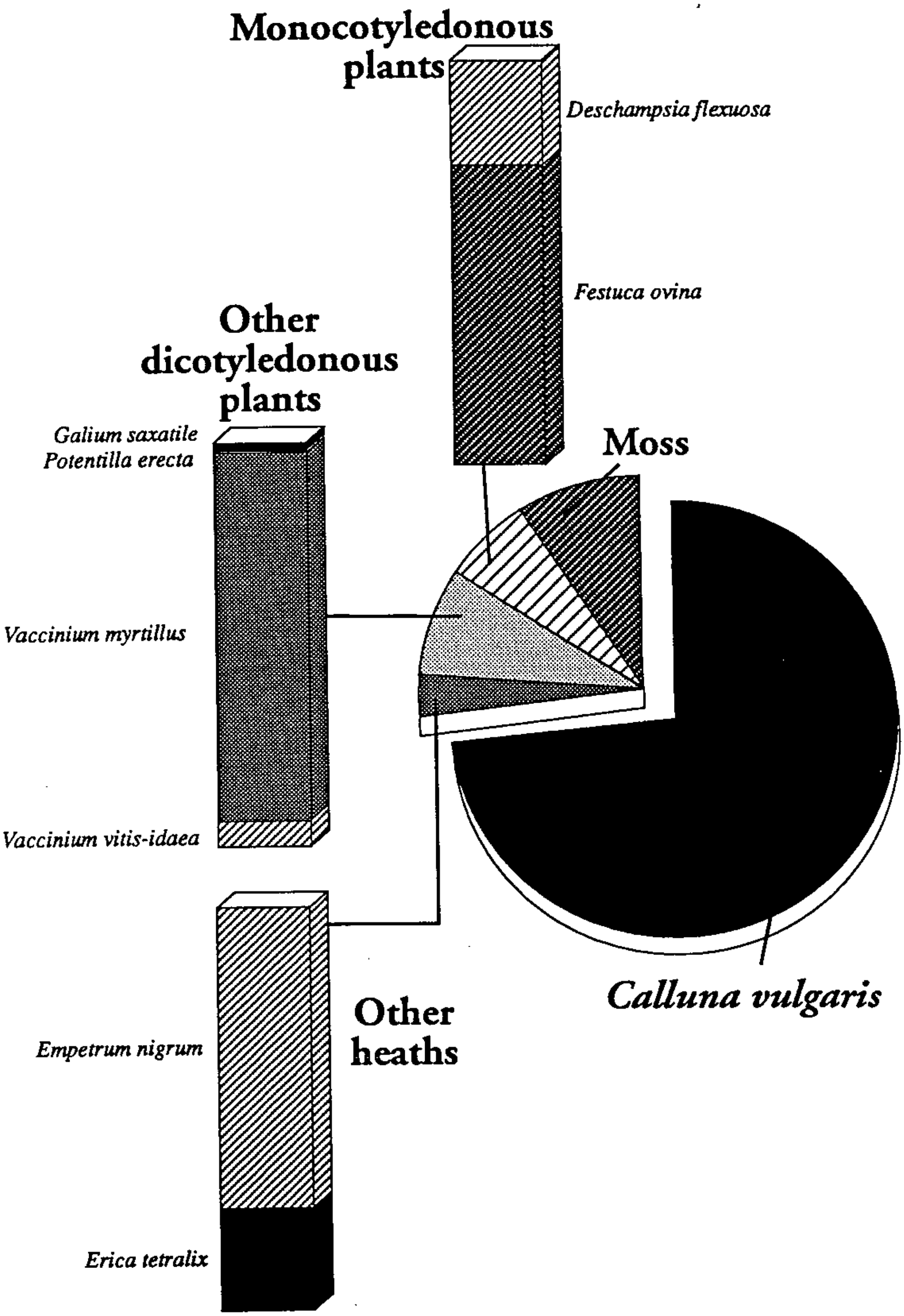


Figure 4.11a: Contribution of individual plant species to the overall composition of the *Calluna* community in summer 1991

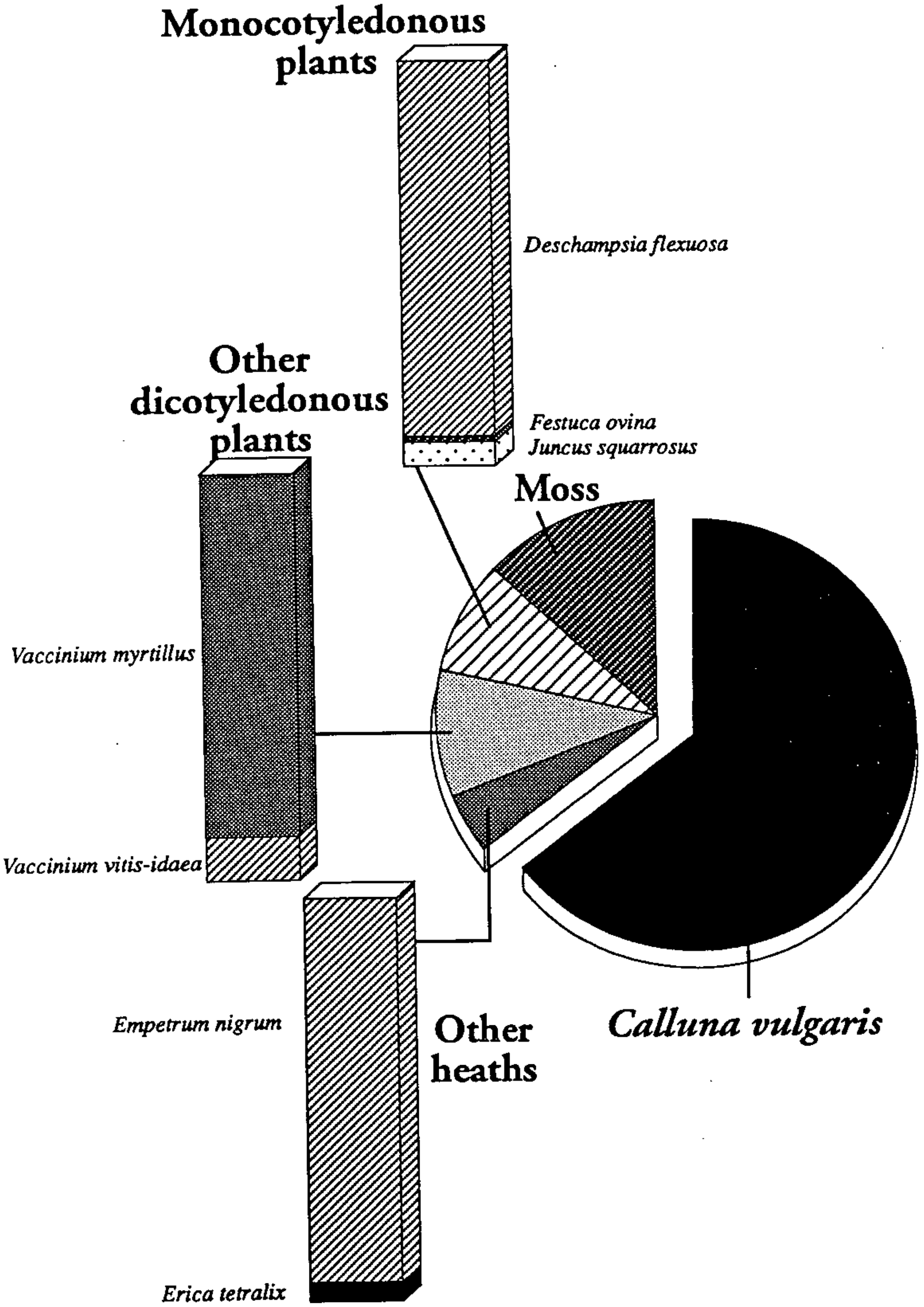


Figure 4.11b: Contribution of individual plant species to the overall composition of the *Calluna* community in spring 1992

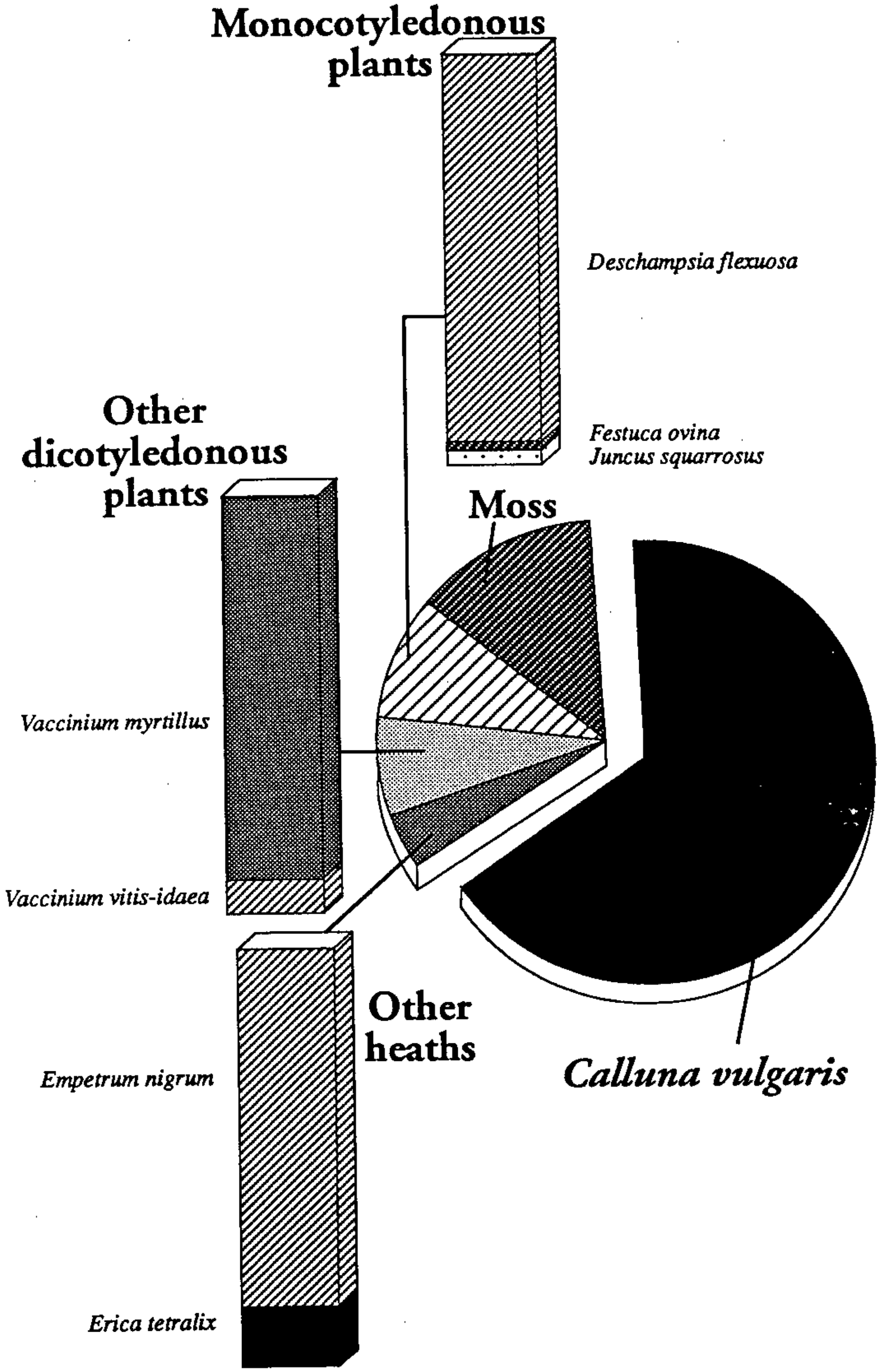


Figure 4.11c: Contribution of individual plant species to the overall composition of the *Calluna* community in summer 1992

the data from the botanical separations. A summary of statistically significant differences is given in Table 4.14. The relative proportions of the morphological units of the four to five *Calluna vulgaris* plants dissected in detail (see Chapter Three) were used to estimate the percentage of the total weight of *Calluna vulgaris* accounted for by each plant part.

Statistically significant differences were found in the proportion of current season's shoots and green old growth between all experimental sessions. However, when these two categories are combined to form one category of green *Calluna vulgaris* leaf comparable with the dietary composition category, no statistically significant differences are evident. A statistically significant difference was found between years in the proportion of *Calluna vulgaris* wood, with summer 1991 being lower than both spring and summer 1992. A seasonal effect was evident in the proportion of *Calluna vulgaris* flowers encountered with samples collected during spring 1992 having significantly lower proportions than those from either summer session.

No differences were found in the percentages of live or dead *Vaccinium* spp. stem, or dead leaves of either *Vaccinium myrtillus* or *Vaccinium vitis-ideae*. Levels of green *Vaccinium myrtillus* leaves were significantly higher in spring 1992 compared with either summer session while levels of green *Vaccinium vitis-ideae* leaves were higher in summer 1991 compared with spring 1992 and summer 1992.

When monocotyledonous plants were considered statistically significant differences were identifiable on two occasions. There was an increased contribution of lamina of fine-leaved grasses in summer 1991 in comparison with summer 1992 while dead *Juncus squarrosus* were more common in summer 1991 than either session in 1992.

The biomass separations were also analysed to obtain an estimate of the *in vitro*

Vegetation category			Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992	
Calluna	shoot	green	ns	ns	ns	
		dead	ns	ns	ns	
	wood		***	***	ns	ψ
	flower		***	***	***	ψ
Erica	all		-	-	-	
Empetrum	all		.	ns	ns	ϕ
V. myrtillus	leaf	green	**	ns	***	
		dead	ns	ns	ns	
V. vitis-idaea	leaf	green	*	*	ns	
		dead	ns	ns	ns	
Vaccinium	stem	green	ns	ns	ns	ψ
		dead	ns	ns	ns	
fine-leaved grass	leaf	green	ns	*	ns	ψ
		dead	ns	ns	ns	
broad-leaved grass	leaf	green	-	-	-	
		dead	-	-	-	
grass vegetative stem			ns	ns	ns	
grass flowerstem			ns	ns	ns	
grass seed/flowerhead			ns	ns	ns	ϕ
Juncus	all	green	ns	ns	ns	
		dead	*	*	ns	
Carex	all	green	ns	ns	ns	
		dead	-	-	-	
Galium	all	green	ns	ns	ns	
		dead	-	-	-	
moss			ns	ns	ns	ϕ

ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$
ϕ = plot effect
ψ = plot x session interaction

Table 4.14: Summary of statistically significant differences between sessions in the contribution of vegetation categories to the overall composition of the Calluna community.

digestibility of each vegetation category during each experimental session (Table 4.15).

4.6.3 Green's index

The Green's index value for each species present is listed in Table 4.16. As anticipated, the value of GI calculated for *Calluna vulgaris* indicated that it was distributed evenly across the measurement area. In 1991 *Calluna* was randomly dispersed and in 1992 the indices of clumping were extremely low. *Empetrum nigra* was more clumped but the GI value was still low. On all three occasions the *Erica tetralix* was the most clumped of the heath species. Both *Vaccinium myrtillus* and *Vaccinium vitis-idaea* were relatively dispersed.

The GI value for *Festuca ovina* was low in 1991 and this species was randomly distributed in both sessions in 1992. There was also little clumping of *Deschampsia flexuosa.* In comparison, when *Agrostis canina*, *Juncus squarrosus*, *Eriophorum angustifolium* and *Galium saxatile* were encountered, they were recorded as occurring in clumps. Moss was distributed evenly.

4.6.4 Sward profile

In comparison with the grass swards the sward-height of the dwarf-shrub community is not influenced by season. Figure 4.12 illustrates the distribution of monocotyledonous and dicotyledonous plants at different horizons in the sward, and contrasts with the equivalent graphs for the two grass swards. With the Calluna community it is the dicotyledonous group which dominates while monocotyledonous plants are restricted to the lower half of the canopy. *Calluna vulgaris* has been plotted separately to emphasis the importance of this species.

Of the height-band profiles which have been created those from the *Calluna vulgaris* data (Figure 4.13) are most easily interpreted as they resemble closely the structure of

Vegetation category			**Summer 1991**	**Spring 1992**	**Summer 1992**
Calluna	current season	green	0.475 ± 0.0077	0.466 ± 0.0010	0.432 ± 0.0123
	old growth	green	0.425 ± 0.0043	0.439 ± 0.0064	0.341 ± 0.0110
		dead	0.307 ± 0.0257	0.301 ± 0.0125	0.248 ± 0.0043
	wood		0.211 ± 0.0260	0.224 ± 0.0215	0.191 ± 0.0068
	flowers		0.335 ± 0.0227	-	0.289 ± 0.0110
Empetrum			0.352	0.274	0.254
Vaccinium	leaf	green	0.411	0.537 ± 0.0270	0.452 ±
	stem	green	0.363 ± 0.0350	0.328 ± 0.0028	0.245 ± 0.0365
		dead	0.247		-
fine-leaved grasses		green	0.605 ± 0.0361	0.597 ± 0.0224	0.649
		dead	0.472	0.346	0.412
vegetative stem			0.451	0.356 ± 0.0392	0.426
moss		green	0.318 ± 0.0098	0.316 ± 0.0054	0.229 ± 0.0024
		dead	0.190	-	-

mean ± s.e.m. across sub-plots

no s.e.m. = value for bulked sample from entire measurement area

\- = insufficient sample

Table 4.9: *In vitro* digestibility values for vegetation categories from the Calluna community during each experimental session.

Species	Summer 1991	Spring 1992	Summer 1992
Calluna vulgaris	0.0003	0.0003	0.0002
Erica cinerea	0.0460	0.1410	0.1008
Vaccinium myrtillus	0.0071	0.0051	0.0058
Vaccinium vitis-idaea	0.0019	0.0183	0.0024
Galium saxatile	-	0.3234	-
Agrostis canina	-	0.9231	0.0633
Deschampsia flexuosa	0.0259	0.0075	0.0040
Festuca ovina	0.0090	-	-
Eriophorum angustifolium	-	-	0.3545
Juncus squarrosus	-	0.3814	0.1143

Values range between 0 - 1: 0 = random and 1 = maximum clumping

Table 4.16: Green's index values for plant species encountered on the Calluna community.

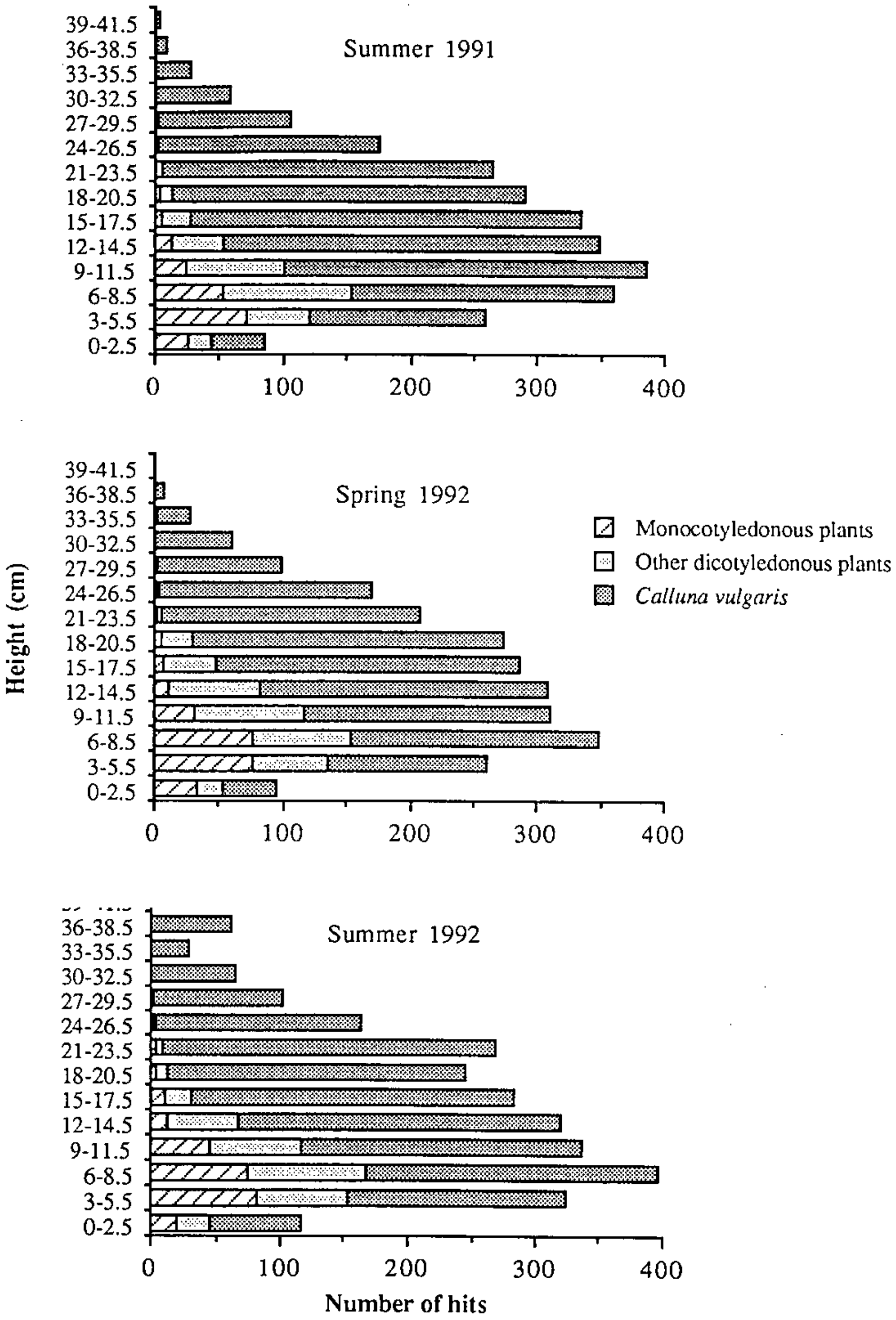


Figure 4.12: Distribution of *Calluna vulgaris*, other dicotyledonous plants and monocotyledonous plants within the Calluna community canopy during each experimental session.

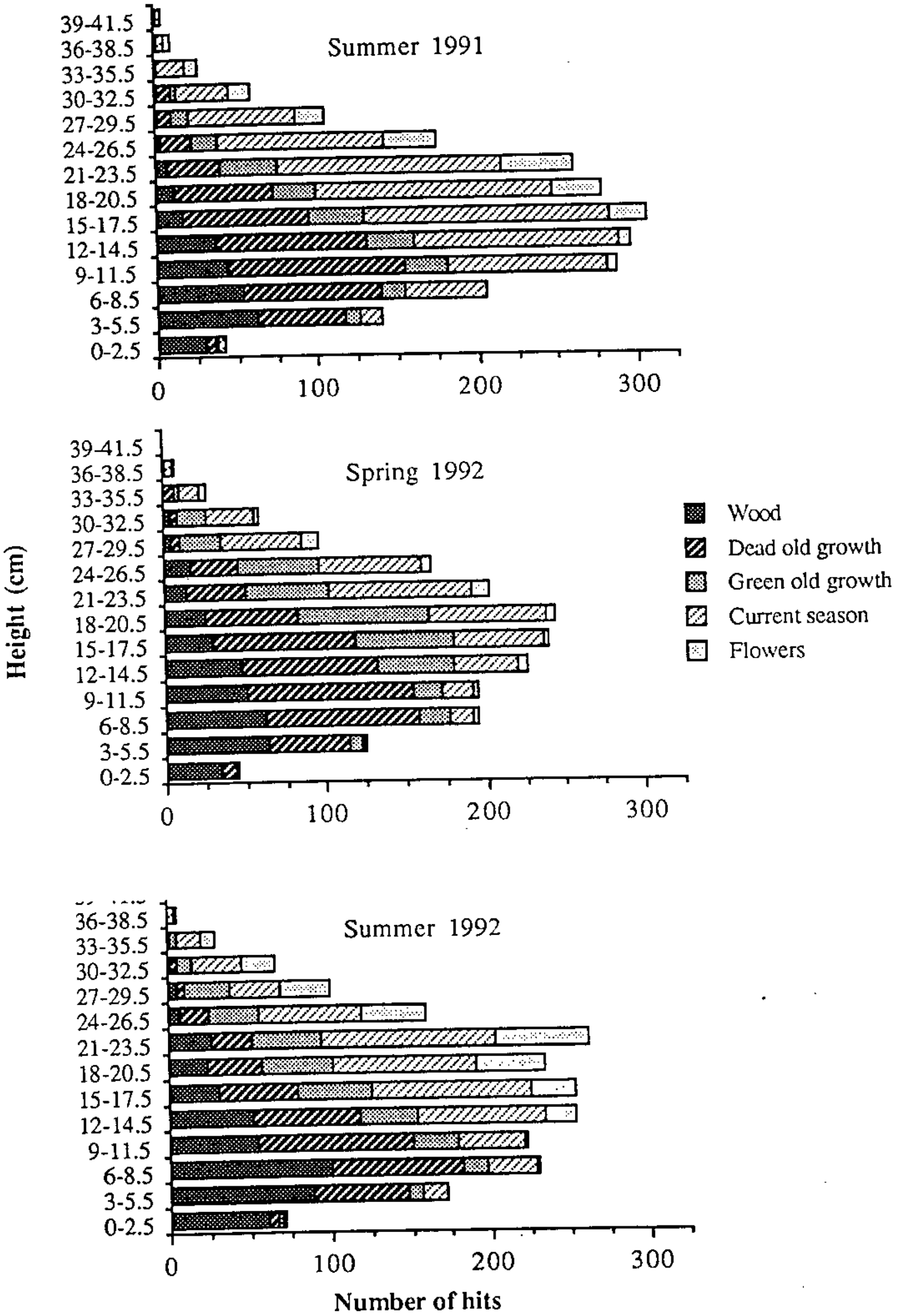


Figure 4.13: Distribution of morphological units of *Calluna vulgaris* within the Calluna community canopy during each experimental session.

the living plant. In particular the pattern of growth is illustrated by each chronologically-consecutive morphological unit being densest at each taller height band. The only seasonal difference was in the contribution of current season's growth and flowers to the summer profiles in comparison with those from the spring .

To summarise the composition and canopy structure of the sward the proportions of the total sward and sward surface accounted for by the equivalent of dietary categories are listed in Table 4.17. It is this data which has been used for comparison with dietary composition in Chapters Five, Six and Seven. Green shoots of *Calluna vulgaris* accounted for between 43-47 per cent of the sward surface yet are never more than 37 per cent of the total sward. There was also a dramatic increase in the percentage of *Calluna vulgaris* flowers at the surface. In contrast there was a reduction in the proportion of dead shoots of *Calluna vulgaris* at the surface compared with the total sward. *Erica* spp. was only encountered once at the sward surface. Other species rarely recorded at the sward surface, if at all, include *Vaccinium vitis-idaea* and *Galium saxatile*. Likewise the proportion of moss was very low in comparison with the whole sward and grass vegetative stem was never recorded.

4.6.5 Biomass

The mean herbage biomass and herbage dry matter for each session are listed in Table 4.18 respectively. There was a statistically significant increase in the herbage biomass of the *Calluna* community during both sessions in 1992 compared with the experimental session in 1991 (compared with spring 1992 $p < 0.01$; compared with summer 1992 $p < 0.01$)

4.7 SUMMARY

1. Attributes which include an ability to tolerate the heavy trampling and defoliation associated with intensive stocking have led to *Lolium perenne* being the most important cultivated graminoid species. However, despite these characteristics sown swards are

			Summer 1991		Spring 1992		Summer 1992	
Vegetation category			Total	Surface	Total	Surface	Total	Surface
Calluna	shoot	green	37.0	57.8	29.8	57.4	27.4	43.3
		dead	21.6	11.9	20.5	12.1	16.2	11.8
	wood		9.0	2.9	12.5	8.0	14.5	8.1
	flower		6.3	18	2.0	7.5	8.2	22.2
Erica	shoot	green	0.5	0	0.1	0	0.4	0.7
Empterum	all		2.0	0.6	3.9	1.9	3.2	1.3
V. myrtillus	leaf	green	3.9	3.4	4.5	5.2	2.4	2.8
		dead	0.5	0.2	0.2	0	0.2	0
V. vitis-idaea	leaf	green	0.4	0	0.7	0.4	0.5	0
Vaccinium	stem	green	2.7	1.7	2.7	1.4	3.7	3.0
		dead	0.7	0.4	0.6	0.4	0.7	0.2
Festuca	leaf	green	2.6	0.8	0	0	0	0
		dead	1.1	0.6	0	0	0.1	0.2
Deschampsia	leaf	green	0.9	0.4	3.9	4.3	3.3	1.9
		dead	0.3	0.4	1.7	0.5	3.8	1.5
grass vegetative stem			1.5	0	2.2	0.0	1.7	0
grass flowerstem			0	0.2	0.7	0	0	0
grass seed/flowerhead			0	0.2	0	0	0	0
Juncus		green	0	0	0.2	0.2	0.2	0
		dead	0	0	0.3	0	0.1	0
Galium	all	green	0.1	0	0	0	0	0
		dead	0.1	0	0.1	0	0	0
moss			8.6	0.9	13.1	0.7	13.2	3.0

Table 4.17: Proportions of total Calluna sward and sward surface only accounted for by categories equivalent to those used during analysis of diet composition.

Session	Herbage biomass (gDM/m2)		Dry matter (%)	
	mean	s.e.m.	mean	s.e.m.
Summer 1991	1316.2	78.48	48.9	8.59
Spring 1992	1736.3	115.87	38.8	12.55
Summer 1992	1761.1	114.52	39.7	14.00

Table 4.18: Herbage biomass (gDM/m2) and herbage dry matter percentage of the Calluna community during each experimental session.

susceptible to invasion as they age: firstly by species such as *Poa annua*, then by *Agrostis* spp. and *Holcus* spp., and eventually by many other indigenous grasses. This process of invasion is reflected in the number of additional species of broad-leaved grasses encountered on the established sown pasture used in this study.

2. Broad-leaved grasses were the main component in the sown sward, with *Trifolium repens* also a consistent contributor. In addition to these components a number of additional species of dicotyledonous plant made minor contributions to the overall sward profile. These were principally opportunistic 'weeds' which had appeared following soil disturbance due to repairs to the drainage system for the pasture.

3. Semi-natural grassland, such as the *Nardus stricta* dominated community used during this project are largely the product of continuous grazing of man's flocks and herds (Grant and Maxwell, 1988). In comparison with sown pasture there was a greater number of vegetation categories in general, and grass types in particular,. which resulted in increased opportunity for selective grazing.

4. Both broad-leaved and fine-leaved grasses were available growing between the distinctive tussocks formed by the dominant species. Also present in these species-rich inter-tussock areas were other monocotyledonous plants, dicotyledonous plants and moss. The degree of clumping of these components varied, increasing the variability of the herbage available.

5. As a dwarf-shrub community the architecture of the *Calluna*-dominated vegetation was very different from that of either grassland community. Such heath moorland can be partitioned into a number of strata. The density and uniformity of the stand depends considerably on its age as well as the environment. In general the density of the second stratum is inversely correlated with that of the one above; and this relationship continues down through the series.

6. The dominant stratum consists mainly of the dwarf-shrub canopy, in this case *Calluna vulgaris*. The second, discontinuous stratum was found beneath and in the gaps of the top stratum and contained partly creeping dwarf-shrubs such as *Empetrum nigrum*, or shorter and less branched species of plants such as *Erica tetralix* and *Vaccinium* spp.. The third stratum contained smaller plants, such as *Galium saxatile*, while the final stratum consists of mat-forming mosses.

CHAPTER FIVE

DIET COMPOSITION AND INGESTIVE BEHAVIOUR OF GOATS

5.1 REVIEW

The goat was one of the first animals to be domesticated, with records indicating their presence as the domesticated form in Egypt from as early as 2700 BC (Merrill and Taylor, 1976). Goats have an ability to thrive in very harsh environments where the rainfall is often below seventy millimetres per year (Devendra, 1978) and this contributes to them having a relatively wide distribution. In contrast to sheep, where sixty per cent of total numbers are found in temperate zones and less than forty per cent in tropical zones, nearly eighty per cent of all goats are found within the band 0 - 40° N, in the arid tropical and subtropical regions (Devendra and Coop, 1982). However, despite its wide distribution and use, Malechek and Provenza (1983) comment that of the important domestic animal species probably least is known about the goat in relation to its numbers and economic importance.

Goats are intermediate feeders under Hofmann's (1973) classification. They have a relatively larger rumen volume than sheep or cattle (Church, 1976; Demment and Van Soest, 1985) and although the evidence is equivocal (Devendra, 1978) recent comparative studies show some differences in the ability of sheep and goats to digest the same forages (Forcant, Vanbelle and Goldroud, 1986; Tolkamp and Brouwer, 1993). Goats and sheep appear to digest high quality forages to a similar extent but goats tend to be more efficient at digesting low quality diets (Louca, Antoniou and Harzipanayiotou 1982; Domingue *et al.*, 1991). Goats also appear to be able to digest forages containing secondary compounds more effectively than sheep (Howe, Barry and Poppi, 1988). This may result from the differential adaption of the goats' rumen microflora (Gihad, El-Bedawy and Mehrez, 1980) and their possessing salivary proteins (Provenza and Malechek, 1984; Robbins *et al.*, 1987) which may nullify the effects of digestion-inhibiting tannins.

One of the main differences between sheep and goats is that, although they both exhibit a mixed foraging strategy, they have differing preferences for grass and browse respectively (Squires, 1982; Bullock, 1985). This in turn can be correlated with additional adaptive diversification. Several morphological features contribute to the goats' successful adaptation to a broad variety of environmental conditions. For example, their narrow incisor arcade and mobile upper lip allows them to select individual species and morphological units of plants (Gordon and Illius, 1988). Likewise goats exhibit a number of behavioural features which contribute to their versatility. For example, being sure-footed allows goats to forage by climbing low trees or on narrow ledges, potentially giving them an advantages over sheep and cattle in having an exclusive food source (Harrington, 1982). Similarly, their ability to assume a bipedal stance can give them exclusive use of a browse stratum unavailable to sheep. Consequently spatial partitioning of the food resource must be taken into consideration when interspecific competition is being evaluated. It has also been suggested that by travelling greater distances than their ruminant counterparts goats increase the opportunity to select a varied diet although this will depend on the dispersion of food items (Huston, 1978).

Van Soest (1987) comments that this versatility and improved performance is characteristic of a response to tropical conditions where morphological partitioning into plant parts of high and low digestibility offers the opportunity for dietary selection by capable species. In contrast, the comparatively nutritively uniform forages which can occur in cooler temperate climates may result in goats not appearing to be very different from other intermediate feeders.

Although reported as having a preference for hilly terrain or areas with tree or shrub cover, this appears to be principally a response to protection from predation and inclement weather rather than as a result of seeking a preferred food source (Harrington, 1982).

As is the case for the majority of herbivores, the common practice of classifying the diet of goats into grass, forbs and browse obscures the fact that each class is comprised of one or more species, each with its own palatability characteristics, and that goats select their diet on a species and plant-part basis. Certainly as a result of their differing preferences there is strong evidence for differences in diet selection between goats and sheep on rangelands (Bullock, 1985; Lu, 1988). In general goats are more catholic in their feeding habits and tend to consume grass and forb species when available and more browse than sheep during the dry season or winter when grass and forbs are limited.

Research suggests that goats may have an important role to play in the control and manipulation of hill communities. The differences recorded in the diet selected when goats were compared with cattle and sheep indicate that they may be a valuable addition to mixed grazing system as an aid to management of the varied plant communities of hill land and particularly in the maintenance and further improvement of reseeded pastures (Russel *et al.*, 1983). Likewise, evidence of an increase in the clover content of pastures grazed by goats has been recorded (McGregor, 1985; Radcfiffe, Townsend and Baird, 1991). Goats have also been used effectively in the control of unwanted plant species, for example, gorse (Radcliffe, 1985; Bullock and Kinnear, 1988).

However, in some parts of the world goats are considered to be highly destructive of vegetation and the principal contributors to severe soil erosion although the views expressed are frequently biased and seldom supported by experimental evidence (Campbell, Ebersohn and Broembsen, 1962). In may situations the main problem is overgrazing due to mismanagement by man.

RESULTS

5.2 DIET COMPOSITION

Variations in the proportion of the diet accounted for by different vegetation categories were in a number of cases identified as resulting from plot effects and/or plot x session interactions, despite the vegetation profiles for the sub-plots being similar (Tables 5.2, 5.5 and 5.8). This suggests that the response of these animals to a given sward can be changeable, and selection for or against particular items unpredictable. Nevertheless, a general picture of the diet most likely to be selected by goats from each community can be created.

5.2.1 The Lolium sward

The mean proportions of the components selected by the goats from the sown sward during each experimental session are tabulated and depicted in Table 5.1 and Figure 5.1 respectively.

On all three occasions the main dietary component was green lamina of broad-leaved grasses; with this vegetation category encompassing around two-thirds of the material consumed. In contrast dead lamina of broad-leaved grasses and other morphological units of grass made only minor contributions to the diet selected.

Dicotyledonous plants accounted for between 18 and 25 per cent of the diet. Once again green leaf was the principal component, with dead leaf, stem and flowers present only in very small quantities if at all. While *Trifolium repens* made a substantial contribution to the diets of the goats during all three experimental sessions, there was a significant increase in the amount of 'other dicotyledonous plants' in the diets selected during both sessions in 1992 in comparison with the diet consumed in summer 1991 (Table 5.2). This inclusion of additional species of dicotyledonous plants resulted in the overall contribution of dicotyledonous plants to the diet increasing during the second year, and was correlated with the significant decrease in green lamina of grass.

The associated Electivity Index values for the categories identified in the diets consumed

Vegetation category			**Summer 1991**	**Spring 1992**	**Summer 1992**
broad-leaved grasses	leaf	green	78.9 ± 6.32	67.3 ± 5.45	64.1 ± 6.61
		dead	1.6 ± 0.34	1.8 ± 0.57	4.8 ± 1.14
grass vegetative stem			0.4 ± 0.10	1.4 ± 0.36	2.3 ± 0.67
grass flowerstem			0.2 ± 0.14	2.2 ± 0.65	1.3 ± 0.40
grass seed/flowerhead			0.5 ± 0.37	2.1 ± 0.60	0.1 ± 0.08
Trifolium repens	leaf	green	17.8 ± 6.03	9.4 ± 2.01	17.4 ± 5.72
		dead	0.2 ± 0.10	0	0.0 ± 0.02
	petiole		0.4 ± 0.16	0.2 ± 0.14	0.8 ± 0.17
	flower		-	-	0
other dicots	leaf	green	0	15.2 ± 6.46	8.0 ± 2.40
		dead	0	0.2 ± 0.14	0.2 ± 0.09
	stem		0	0.3 ± 0.16	0.6 ± 0.41
	flower		-	0	0.3 ± 0.12
			n = 12	n = 17	n = 15

0 = recorded in vegetation but not in diet. - = absent from vegetation and diet.

All results expressed as mean percentage ± s.e.m.

Table 5.1: Composition of the diets consumed by the goats on the Lolium community.

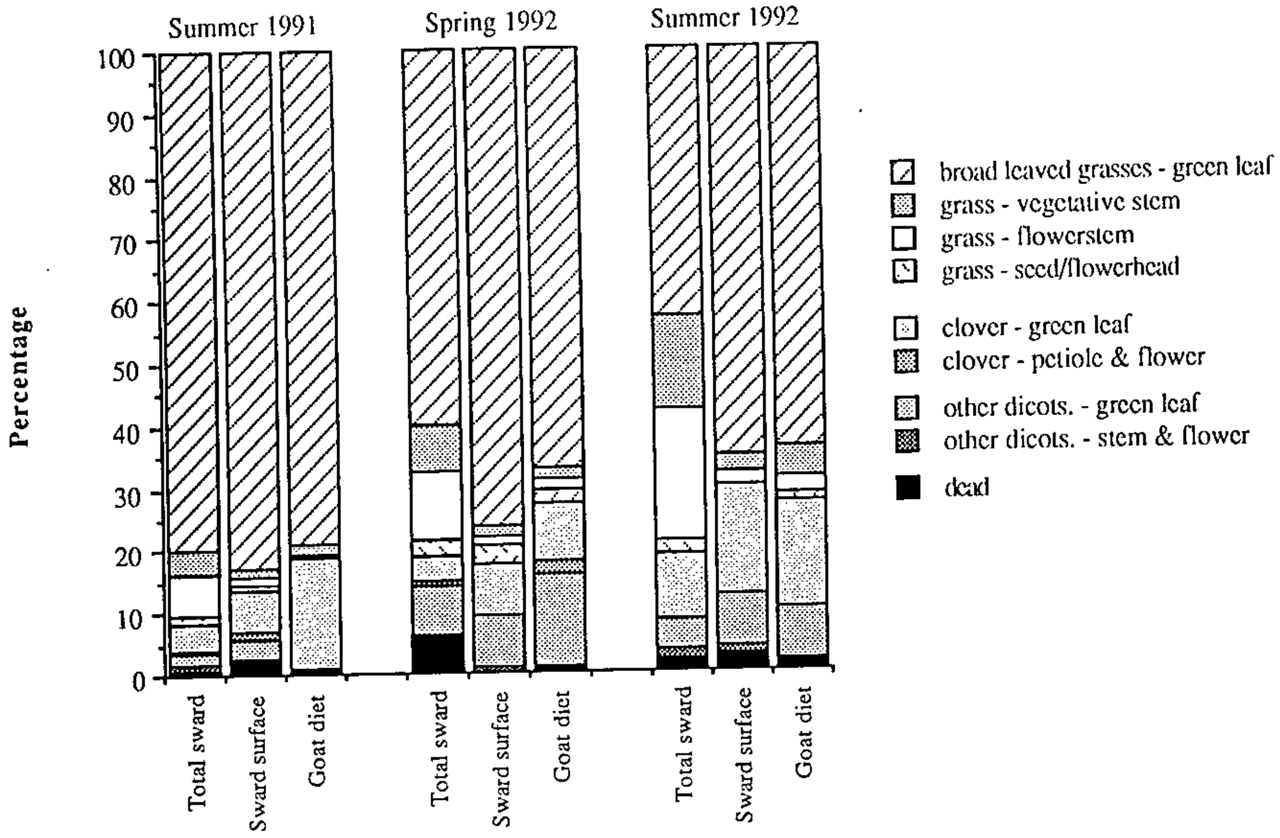


Figure 5.1: Composition of the diets consumed by the goats on the Lolium sward.

Vegetation category			**Summer 1991 v. Spring 1992**	**Summer 1991 v. Summer 1992**	**Spring 1992 v. Summer 1992**	
broad-leaved grasses	leaf	green	*	*	ns	φψ
		dead	ns	*	**	
grass vegetative stem			ns	***	ns	φψ
grass flowerstem			**	*	ns	φψ
grass seed/flowerhead			**	ns	***	
Trifolium repens	leaf	green	ns	ns	ns	ψ
		dead	**	*	ns	φψ
	petiole		ns	*	***	ψ
other dicots	leaf	green	***	*	ns	φψ
		dead	ns	ns	ns	
	stem		ns	ns	ns	
	flower		ns	**	**	

ns = not significant; * = p<0.05; ** = p<0.01; *** = p<0.001
φ = plot effect
ψ = plot x session interaction

Table 5.2: Summary of statistical analysis comparing the diets selected by the goats from the Lolium sward during each experimental session

on the Lolium sward are listed in Table 5.3. No clear pattern can be identified in the response of the goats to the various vegetation categories encountered. Despite green lamina of broad-leaved grasses accounting for over 60 per cent of the material consumed, this component was only tolerated or weakly selected in comparison with availability in the sward as a whole, and tolerated or weakly avoided relative to the composition of the sward surface. Selection and avoidance of dead lamina, flowerstem and seed/flowerhead of grasses also varied between sessions, whereas the avoidance of grass vegetative stem was comparatively consistent. The levels of green clover leaf in the diet indicated there had been positive and neutral selection for this component relative to its availability in the total sward and at the sward surface respectively. Selectivity for the dead clover leaf, petiole and flowers varied. Likewise, selection for and against green and dead leaves of other dicotyledonous plants was unpredictable while there was sustained avoidance of stem.

5.2.2 The Nardus community

The mean proportions of components in the diet selected from the indigenous grassland community on each occasion are tabulated and depicted in Table 5.4 and Figure 5.2 respectively.

There was a pronounced seasonality in the diet composition of the goats on the Nardus sward. While the main component in the diet selected during each experimental session remained green lamina of broad-leaved grasses, the level in the spring 1992 diet was significantly lower than that recorded during either summer session (Table 5.5). Conversely there was a pronounced increase in the amount of *Luzula* spp. in the diet consumed during this experimental session resulting in this component accounting for over 20 per cent of the material consumed. There was also an increase in the proportion of green lamina of *Nardus stricta* from well below 1 per cent to almost 5 per cent. In contrast there was no evidence of a seasonal shift in the contribution of green and dead

Vegetation category			**Summer 1991**		**Spring 1992**		**Summer 1992**	
			Total	**Surface**	**Total**	**Surface**	**Total**	**Surface**
broad-leaved grasses	leaf	green	0	-	+	-	+	0
		dead	-	-	- -	+ +	- -	+
grass vegetative stem			- -	-	- -	-	- -	0
grass flowerstem			- -	- -	-	+	-	-
grass seed/flowerhead			+	-	+	-	+	+ +
Trifolium repens	leaf	green	+ +	+ +	+	0	+	0
		dead	-	+ +	- -		- -	+ +
	petiole		-	-	+	+ +	-	+ +
	flower						- -	
other dicots	leaf	green	- -	- -	+	+	+	0
		dead	- -		- -	+ +	-	+ +
	stem		- -	- -	- -	-	-	-
	flower				- -	- -	+ +	+ +

Abbreviations: + + = strong selection; + = weak selection; 0 = indifference; - = weak avoidance; - - = strong avoidance; blank = absent from vegetation and diet. Total = relative to proportion in total sward. Surface = relative to proportion at sward surface.

Table 5.3: Selectivity indices for goat diets from the Lolium sward.

Vegetation category			Summer 1991	Spring 1992	Summer 1992
Nardus	leaf	green	0.2 ± 0.09	4.9 ± 1.44	0.0 ± 0.02
		dead	0.0 ± 0.04	0.4 ± 0.20	0.1 ± 0.07
broad-leaved grasses	leaf	green	62.8 ± 7.03	36.8 ± 6.37	79.8 ± 3.33
		dead	3.9 ± 0.85	9.4 ± 1.04	8.0 ± 0.90
Festuca	leaf	green	1.1 ± 0.38	0.6 ± 0.24	0.2 ± 0.16
		dead	0.2 ± 0.10	0.3 ± 0.11	0.0 ± 0.02
Deschampsia	leaf	green	1.2 ± 0.36	3.3 ± 0.76	2.2 ± 0.92
		dead	0.1 ± 0.08	0.9 ± 0.29	0.2 ± 0.11
grass vegetative stem			2.0 ± 0.34	3.5 ± 0.56	1.6 ± 0.38
grass flowerstem			2.5 ± 0.85	3.8 ± 0.69	3.1 ± 0.63
grass seed/flowerhead			17.2 ± 6.85	1.0 ± 0.60	1.3 ± 0.41
Carex	all	green	0	0.1 ± 0.06	0
		dead	-	0	-
Luzula	flower		-	1.8 ± 0.96	-
	leaf	green	0.9 ± 0.62	21.5 ± 6.49	2.5 ± 2.03
		dead	0.2 ± 0.15	7.0 ± 1.94	0.6 ± 0.34
other monocots.	all	green	0	-	0
		dead	0	-	0
Galium	all	green	2.4 ± 1.32	0.3 ± 0.21	0.2 ± 0.12
		dead	0.0 ± 0.02	±	0.0 ± 0.02
Vaccinium	all	green	0.0 ± 0.02	2.0 ± 1.11	0.0 ± 0.04
		dead	0.0 ± 0.04	2.2 ± 1.78	0
Potentilla	all	green	2.6 ± 1.83	0	0
		dead	0.1 ± 0.09	0	-
Campanula	all	green	2.4 ± 2.35	-	-
other dicots.	all	green	0	-	0
moss			0.1 ± 0.04	0.3 ± 0.16	0
			n = 13	n = 16	n = 15

0 = recorded in vegetation but not in diet. - = absent from vegetation and diet.

All results expressed as mean percentage ± s.e.m.

Table 5.4: Composition of the diets consumed by the goats on the Nardus community.

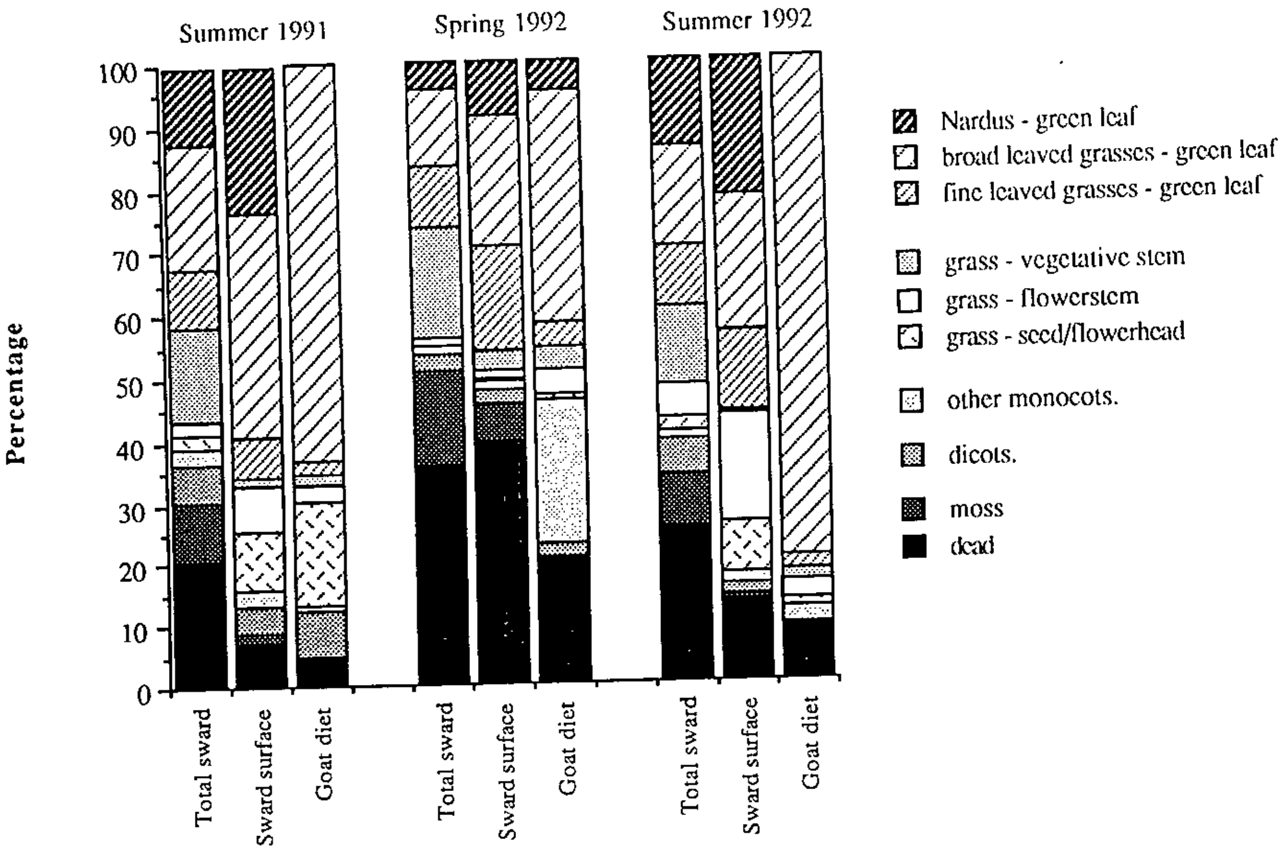


Figure 5.2: Composition of the diets consumed by the goats on the Nardus community.

Vegetation category			Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992	
Nardus	leaf	green	***	ns	***	φψ
		dead	ns	ns	ns	
broad-leaved grasses	leaf	green	***	*	***	ψ
		dead	***	**	ns	ψ
Festuca	leaf	green	ns	ns	ns	
		dead	ns	ns	ns	
Deschampsia	leaf	green	ns	ns	ns	
		dead	**	ns	*	
grass vegetative stem			*	ns	***	φψ
grass flowerstem			*	ns	ns	φ
grass seed/flowerhead			***	***	ns	φψ
Carex	all	green	ns	ns	ns	
Luzula	flower		***	ns	***	φψ
	leaf	green	***	ns	***	φψ
		dead	***	ns	***	φψ
Galium	all	green	ns	ns	ns	
		dead	ns	ns	ns	
Vaccinium	all	green	**	ns	***	φψ
		dead	ns	ns	ns	
Potentilla	all	green	**	**	ns	
		dead	*	*	ns	
Campanula	all	green	ns	ns	ns	ψ
moss			ns	ns	*	

ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$

φ = plot effect

ψ = plot x session interaction

Table 5.5: Summary of statistical analysis comparing the diets selected by the goats from the Nardus community during each experimental session.

lamina of either *Festuca ovina* or *Deschampsia flexuosa*. Likewise the levels of grass vegetative stem and flowerstem were consistently low and although seed/flowerhead made a substantial contribution to the diet in summer 1991 this was not sustained in either session in 1992. The levels of dicotyledonous plants in the diet were low on all three occasions.

The Electivity Index values for the dietary components selected from the Nardus community are listed in Table 5.6. The significantly higher proportion of green lamina of *Nardus stricta* recorded for the spring 1992 diet is associated with a switch from strong avoidance to tolerance of this component in its early growth phase. In contrast, despite the significant differences in the amount of green lamina of broad-leaved grasses there was consistent strong selection relative to the availability of this component in the sward as a whole. Selection of dead lamina of broad-leaved grasses also occurred, contrasting with the response of the goats to this vegetation category when grazing on the Lolium sward. In general there was an avoidance of *Festuca ovina*, while the selectivity indices for *Deschampsia flexuosa* were variable.

There was avoidance of vegetative stem in the sward as a whole, while, in contrast, selection occurred relative to the availability of this component at the sward surface. This contrasts with the results from the sown pasture where vegetative stem was consistently avoided. Although the selectivity indices for grass flowerstem in summer 1991 differed from those of seed/flowerhead with the goats avoiding stem but selecting seed/flowerhead, during the experimental sessions in 1992 the selection and avoidance of these components were similar.

The significant increase in the contribution of all parts of *Luzula* spp. to the spring 1992 diet was associated with consistent strong selection for these components at that time. In contrast, sedges were consistently avoided. There is no consistent pattern in the selection

Vegetation category			Summer 1991		Spring 1992		Summer 1992	
			Total	**Surface**	**Total**	**Surface**	**Total**	**Surface**
Nardus	leaf	green	- -	- -	0	-	- -	- -
		dead	- -	- -	- -	- -	- -	- -
broad-leaved	leaf	green	+ +	+ +	+ +	+	+ +	+ +
grasses		dead	0	+ +	+	+	+	+ +
Festuca	leaf	green	- -	- -	- -	- -	- -	- -
		dead	- -	+ +	- -	- -	- -	- -
Deschampsia	leaf	green	- -	-	0	-	+	-
		dead	- -	-	0	+	-	+ +
grass vegetative stem			- -	+	- -	+	- -	+ +
grass flowerstem			0	- -	+ +	+	-	- -
grass seed/flowerhead			+ +	+	+ +	+	-	- -
Carex	all	green	- -		-	- -	- -	- -
		dead			- -	- -		
Luzula	flower				+ +	+ +		
	leaf	green	-	-	+ +	+ +	+	+
		dead	- -	+ +	+ +	+ +	-	+
other monocots.	all	green	- -				- -	
		dead	- -				- -	
Galium	all	grean	-	0	- -	- -	- -	- -
		dead	- -	- -			- -	+ +
Vaccinium	all	green	- -	- -	+ +	+ +	- -	+ +
		dead	-		+ +	+ +	- -	
Potentilla	all	green	+	+ +	- -	- -	- -	- -
		dead	+	+ +	- -			
Campanula	all	green	+ +	+ +				
other dicots.	all	green	- -	- -			- -	
moss			- -	- -	- -	- -	- -	- -

Abbreviations: + + = strong selection; + = weak selection; 0 = indifference; - = weak avoidance; - - = strong avoidance; blank = absent from vegetation and diet. Total = relative to proportion in total sward. Surface = relative to proportion at sward surface.

Table 5.6: Selectivity indices for goat diets from the Nardus community.

or avoidance of the categories of dicotyledonous plants between sessions, nor can variations be attributed to seasonal differences.

5.2.3 The Calluna community

The mean proportions of components in the diet selected by the goats from the dwarf-shrub community on each occasion are tabulated and depicted in Table 5.7 and Figure 5.3 respectively.

The number and variety of vegetation categories making a substantial contribution to the overall diet consumed increased on the Calluna community in comparison with the grassland communities. Thus instead of one category accounting for the bulk of the material consumed as was found when the goats selected from the grass swards, the proportion of the diet accounted for by the main dietary component never exceeded thirty per cent.

Green shoots were the only component of *Calluna vulgaris* which made a consistent contribution to the diet selected during each experimental session, ranging from just over 5 per cent in spring 1992 to 18 per cent in summer 1992. In contrast, the levels of dead shoots and wood in the diet were lower than 2 per cent on all three occasions. The percentages of *Calluna vulgaris* flower in the diets selected in summer 1991 and spring 1992 were also low, yet during summer 1992 this component accounted for over 11 per cent of the overall diet.

While green and dead leaves of *Vaccinium myrtillus* were a major dietary component, leaves of *Vaccinium vitis-idaea* were consumed only in minor quantities or omitted. Green *Vaccinium* stem accounted for up to 7 per cent of the diet yet the amount of dead *Vaccinium* stem recorded was negligible.

Vegetation category			Summer 1991	Spring 1992	Summer 1992
Calluna	shoot	green	13.1 ± 2.81	5.2 ± 2.22	18.0 ± 4.49
		dead	1.2 ± 0.25	1.1 ± 0.58	1.7 ± 0.50
	wood		0.6 ± 0.20	0.1 ± 0.08	1.2 ± 0.31
	flower		1.4 ± 0.62	0.4 ± 0.19	11.2 ± 3.05
Erica	shoot	green	1.7 ± 1.38	1.4 ± 1.19	2.9 ± 1.13
		dead	0.1 ± 0.08	0.2 ± 0.15	0.1 ± 0.06
	wood		0.6 ± 0.56	0.2 ± 0.14	0.4 ± 0.42
	flower		0	1.1 ± 0.71	0.2 ± 0.16
Empetrum			0	0	0
V. myrtillus	leaf	green	4.9 ± 1.80	21.6 ± 6.43	13.9 ± 2.86
		dead	12.4 ± 4.15	7.0 ± 1.70	11.7 ± 3.28
	flower		-	0.2 ± 0.15	-
V. vitis-idaea	leaf	green	0.4 ± 0.34	0	0.3 ± 0.19
		dead	0	-	0
Vaccinium	stem	green	7.0 ± 2.31	3.3 ± 1.08	6.2 ± 1.39
		dead	0.4 ± 0.20	0.2 ± 0.17	0.4 ± 0.16
Festuca	leaf	green	26.5 ± 4.58	29.4 ± 7.28	16.3 ± 5.50
		dead	12.2 ± 2.47	4.4 ± 0.97	8.1 ± 2.52
Deschampsia	leaf	green	0	0.1 ± 0.08	0
		dead	0	0	0
broad-leaved grass	leaf	green	9.6 ± 6.09	7.2 ± 2.24	0.6 ± 0.33
		dead	4.7 ± 2.06	3.3 ± 1.22	0.4 ± 0.21
grass vegetative stem			0.4 ± 0.24	5.5 ± 2.23	0.4 ± 0.18
grass flower stem			1.6 ± 0.23	4.1 ± 0.78	0.7 ± 0.32
grass seed/flowerhead			0.2 ± 0.16	2.1 ± 0.99	-
Juncus		green	-	0.9 ± 0.09	0
		dead	-	0.0 ± 0.03	0
Galium		green	0	0.1 ± 0.06	0
		dead	0	0.0 ± 0.03	-
other dicot.		green	0.1 ± 0.14	-	-
moss			1.2 ± 0.52	1.1 ± 0.74	5.6 ± 4.42
			n = 11	n = 12	n = 15

0 = recorded in vegetation but not in diet. - = absent from vegetation and diet.
All results expressed as mean percentage ± s.e.m.

Table 5.7: Composition of the diets consumed by the goats on the Calluna community.

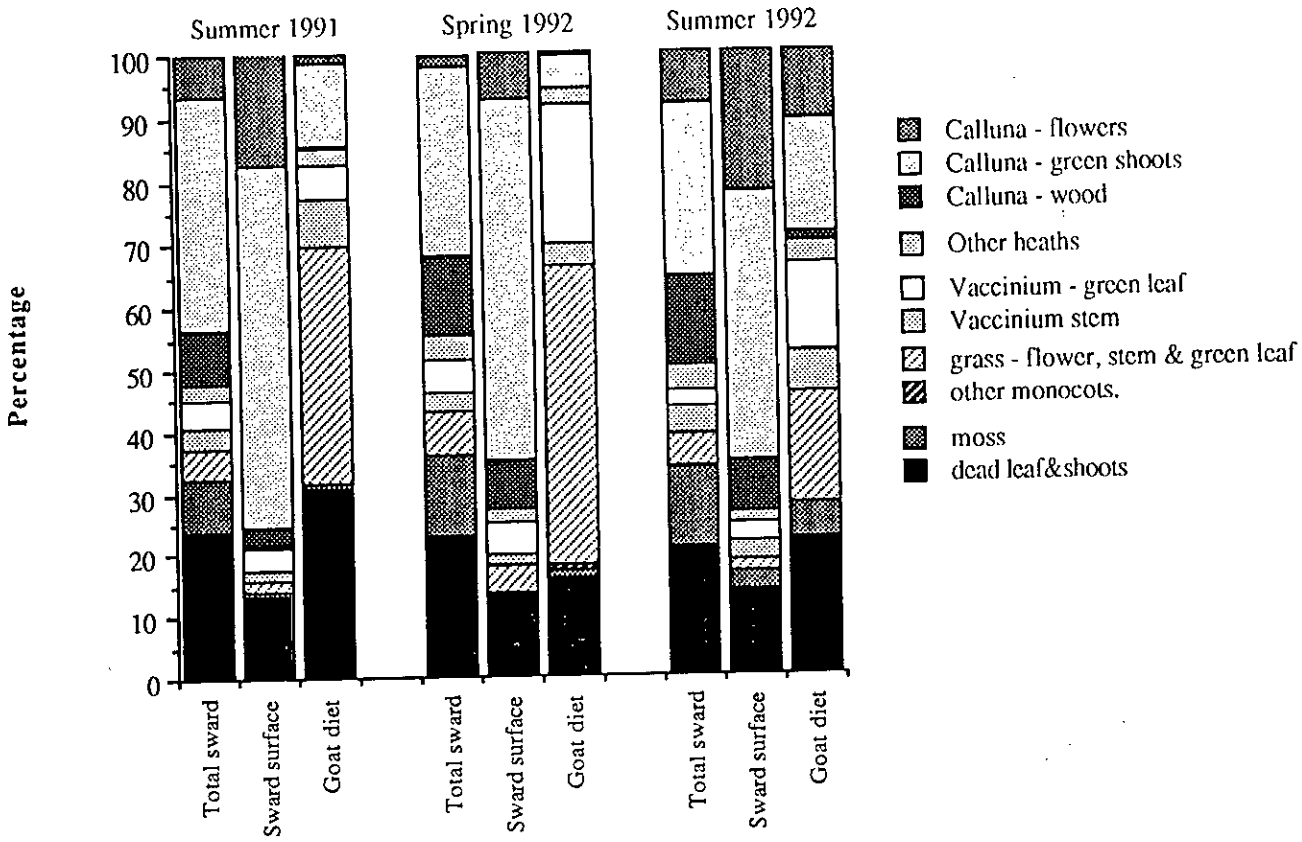


Figure 5.3: Composition of the diets consumed by the goats on the Calluna community.

Green and dead lamina of *Festuca ovina* in the diets accounted for between 16-30 and 4-12 per cent of the material consumed respectively. However, although these and equivalent categories of broad-leaved grasses were significantly lower in summer 1992 than during either of the previous experimental sessions (Table 5.8), the levels of grass vegetative stem, flowerstem and seed/flowerhead were all significantly higher during the spring experimental session. Green and dead lamina of *Deschampsia flexuosa* was all but omitted from the diet.

The corresponding Electivity Index values for each component are listed in Table 5.9. When compared with the selectivity indices for the various vegetation categories available on the grassland communities, it can be seen that selection for or against the same component during different sessions was most consistent on the Calluna community. In general all morphological units of the dominant species were avoided, yet those of *Erica* spp. selected. Green and dead leaves of *Vaccinium myrtillus* were selected along with green *Vaccinium* spp. stem, whereas dead *Vaccinium* spp. stem and the response to leaves of *Vaccinium vitis-idaea* varied.

With the exception of lamina of *Deschampsia flexuosa* all grass categories were selected. In contrast, selection for and against *Juncus* spp. and the species of forbs present varied. Although moss was avoided relative to the proportion of this component in the sward as a whole, weak selection occurred in comparison with the availability at the sward surface.

5.3 DIET DIGESTIBILITY

5.3.1 *In vitro* digestibility

The mean digestibility of the diets selected from each community by the oesophageal fistulates during each experimental session are listed in Table 5.10a and plotted in Figure 5.4a. Summaries of statistically significant differences are given in Table 5.10b and 5.10c.

Vegetation category			Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992	
Calluna	shoot	green	*	ns	**	ψ
		dead	ns	ns	ns	
	wood		ns	ns	**	
	flower		ns	***	***	φψ
Erica	shoot	green	ns	ns	ns	
		dead	ns	ns	ns	
	wood		ns	ns	ns	
	flower		*	ns	ns	
V. myrtillus	leaf	green	ns	ns	ns	
		dead	ns	ns	ns	
	flower		*	ns	*	ψ
V. vitis-idaea	leaf	green	ns	ns	ns	
		dead	-	-	-	
Vaccinium	stem	green	ns	ns	ns	
		dead	ns	ns	ns	
Festuca	leaf	green	ns	*	*	ψ
		dead	***	**	ns	φψ
Deschampsia	leaf	green	ns	ns	ns	
broad-leaved grass	leaf	green	ns	*	**	ψ
		dead	ns	**	**	ψ
grass vegetative stem			*	ns	***	
grass flower stem			***	ns	***	φψ
grass seed/flowerhead			***	ns	***	φψ
Juncus		green	ns	ns	ns	
		dead	ns	ns	ns	
Galium		green	ns	ns	ns	
		dead	ns	ns	ns	
other dicot.		green	ns	ns	ns	
moss			ns	ns	ns	φ

ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$
φ = plot effect
ψ = plot x session interaction

Table 5.8: Summary of statistical analysis comparing the diets selected by the goats from the Calluna community during each experimental session

Vegetation category			**Summer 1991**		**Spring 1992**		**Summer 1992**	
			Total	**Surface**	**Total**	**Surface**	**Total**	**Surface**
Calluna	shoot	green	- -	- -	- -	- -	-	- -
		dead	- -	- -	- -	- -	- -	- -
	wood		- -	- -	- -	- -	- -	- -
	flower		- -	- -	- -	- -	+	-
Erica	shoot	green	+ +	+ +	+ +	+ +	+ +	+ +
		dead	+ +	+ +	+ +	+ +	+ +	+ +
	wood		+ +	+ +	+ +	+ +	+ +	+ +
	flower		- -		+ +	+ +	+ +	+ +
Empetrum			- -	- -	- -	- -	- -	- -
V. myrtillus	leaf	green	+	+	+ +	+ +	+ +	+ +
		dead	+ +	+ +	+ +	+ +	+ +	+ +
	flower				+ +	+ +		
V. vitis-idaea	leaf	green	0	+ +	- -	- -	-	+ +
		dead	- -				- -	
Vaccinium	stem	green	+	+ +	+	+	+	+
		dead	-	0	-	-	-	+
Festuca	leaf	green	+ +	+ +	+ +	+ +	+ +	+ +
		dead	+ +	+ +	+ +	+ +	+ +	+ +
Deschampsia	leaf	green	- -	- -	- -	- -	- -	- -
		dead	- -	- -	- -	- -	- -	- -
broad-leaved grass	leaf	green	+ +	+ +	+ +	+ +	+ +	+ +
		dead	+ +	+ +	+ +	+ +	+ +	+ +
grass vegetative stem			0	+ +	+	+ +	-	+ +
grass flower stem			+ +	+	+ +	+ +	+ +	+ +
grass seed/flowerhead			+ +	0	+ +	+ +		
Juncus		green			+ +	+ +	- -	
		dead			- -	+ +	- -	
Galium		green	- -		+ +	+ +	- -	
		dead	- -		-	+ +		
other dicot.		green	+ +	+ +				
moss			- -	+	- -	+	-	+

Abbreviations: + + = strong selection; + = weak selection; 0 = indifference; - = weak avoidance; - - = strong avoidance; blank = absent from vegetation and diet.
Total = relative to proportion in total sward. Surface = relative to proportion at sward surface.

Table 5.9: Selectivity indices for goat diets from the Calluna community.

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	0.784 ± 0.0059	0.806 ± 0.0103	0.802 ± 0.0086
Nardus	0.655 ± 0.0137	0.656 ± 0.0102	0.632 ± 0.0106
Calluna	0.501 ± 0.0213	0.668 ± 0.0141	0.441 ± 0.0234

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	ns	ns	ns
Nardus	ns	ns	ns
Calluna	***	**	***

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	***	***	***
Spring 1992	***	***	ns
Summer 1992	***	***	***

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 5.10: *In vitro* digestibility of diets selected by goats.

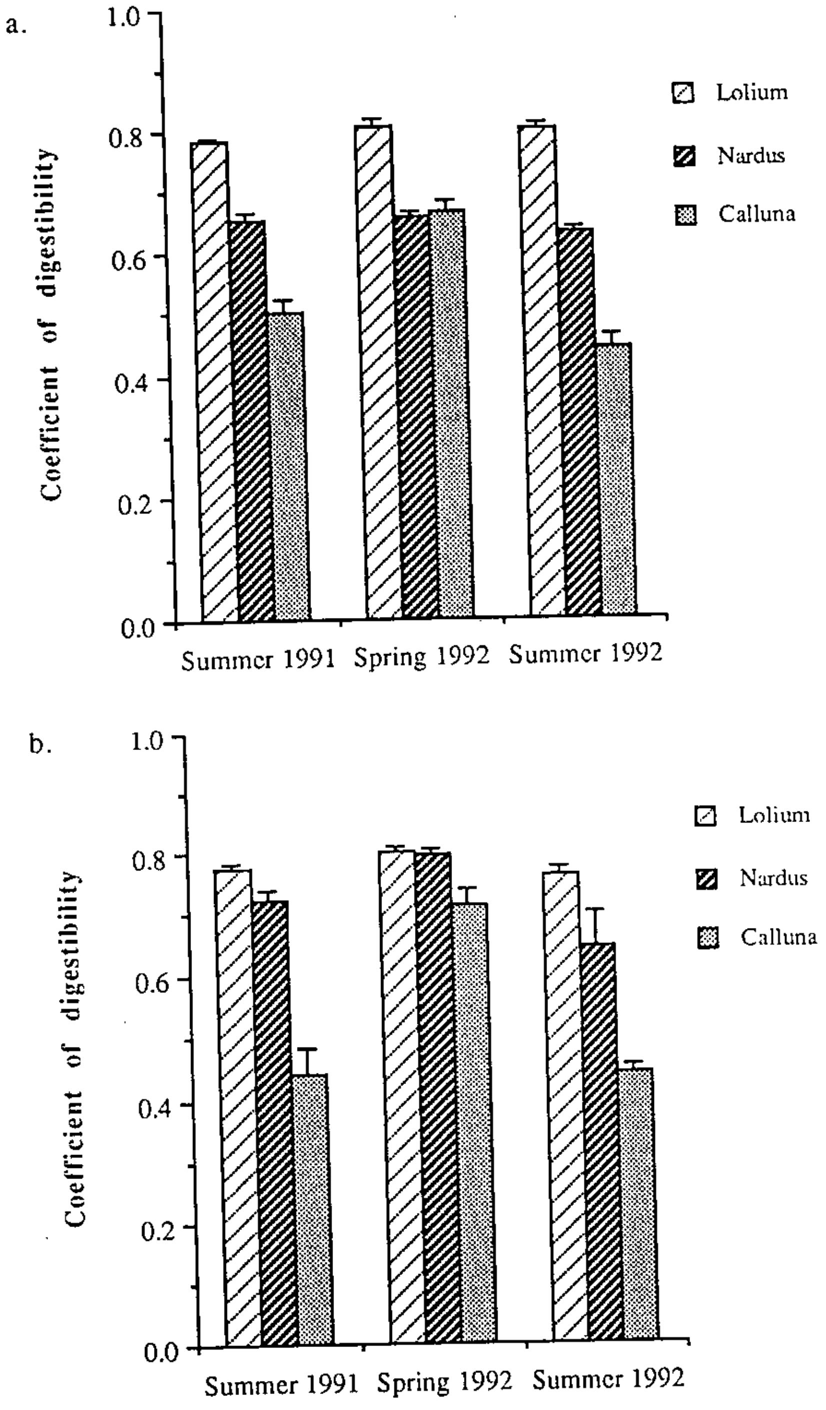


Figure 5.4: Effect of season and vegetation type on digestibility of diets selected by goats as determined using: a. *in vitro* analysis; b. n-alkane analysis.

There were no significant differences in *in vitro* digestibility between the diet selected from the Lolium sward during each session. Likewise, the digestibility of the diets consumed on the Nardus community were similar. The diet selected from the Calluna community in spring 1992 had a significantly higher coefficient of digestibility than that selected in summer 1991 which in turn was significantly higher than the value for the diet consumed in summer 1992.

The *in vitro* digestibility of the diet selected from the Lolium sward was consistently significantly higher than those from the indigenous communities. During the summer experimental sessions the diet consumed on the Nardus community had a significantly higher coefficient of digestibility than the diet selected from the Calluna community. In comparison the significant increase in digestibility of the Calluna diet in spring corresponded to there no longer being a difference.

5.3.2 Digestibility from n-alkanes

Equivalent results and statistical information for diet digestibility as determined using the n-alkane technique for intact animals grazing the same communities have been plotted and tabulated in Figure 5.4b and Table 5.11a, 5.11b and 5.11c respectively. Once again there were no significant differences in the digestibility of the diet selected from the Lolium sward during each experimental session. However, a significant difference between the spring 1992 and summer 1992 diets selected from the Nardus community was recorded; while conversely a significant difference between the diets consumed in summer 1991 and summer 1992 on the Calluna vegetation identified in the *in vitro* results was no longer detected.

Considering differences between communities, the digestibility of the diets consumed on the Lolium and Nardus swards in summer 1991 were similar whereas the digestibility of the material consumed on the dwarf-shrub community was significantly lower then that

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	0.777 ± 0.0083	0.802 ± 0.0078	0.761 ± 0.0133
Nardus	0.723 ± 0.0182	0.795 ± 0.0111	0.645 ± 0.0571
Calluna	0.441 ± 0.0417	0.716 ± 0.0264	0.442 ± 0.0113

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	ns	ns	ns
Nardus	ns	ns	**
Calluna	***	ns	***

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	ns	***	***
Spring 1992	ns	*	ns
Summer 1992	*	***	***

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 5.11: Digestibility of diets selected by goats as determined using n-alkanes.

on either grass community. Only the digestibility of the Lolium diet was significantly higher than that of the Calluna diet in spring 1992. In summer 1992 there were significant differences between all three, with the digestibility of the Lolium and Calluna diets having the highest and lowest values respectively.

5.4 INTAKE

5.4.1 Organic matter intake

The organic matter intake (OMI) of the goats on each community during each experimental session are listed in Table 5.12a and plotted in Figure 5.5a. Statistical differences are summarised in Table 5.12b and 5.12c.

No differences were recorded between experimental sessions in the amount consumed on the Lolium sward. In contrast, on both the Nardus and Calluna communities the intake of the goats was significantly higher during the spring session.

During the session in summer 1991 OMI was higher on the Nardus grassland than on the Lolium sward or Calluna community. This was repeated in spring 1992 and in addition intake on the Calluna community was significantly higher than that on the Lolium sward. While no difference was detected between the amounts consumed on the Lolium and Nardus or Lolium and Calluna communities during the third session, once again the OMI of the goats was significantly higher on the Nardus community than on the Calluna community.

5.5.2 Digestible organic matter intake

The digestible organic matter intake (DOMI) during each experimental session is summarised in Table 5.13a and plotted in Figure 5.5b. Summaries of statistically significant differences are given in Table 5.13b and 5.13c.

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	0.907 ± 0.0781	1.042 ± 0.1321	1.040 ± 0.0606
Nardus	1.348 ± 0.1187	2.245 ± 0.1469	1.269 ± 0.1582
Calluna	0.646 ± 0.0826	1.431 ± 0.1587	0.723 ± 0.0367

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	ns	ns	ns
Nardus	***	ns	***
Calluna	**	ns	**

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	*	ns	**
Spring 1992	***	*	***
Summer 1992	ns	ns	**

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 5.12: Organic matter intake of goats (kg/day)

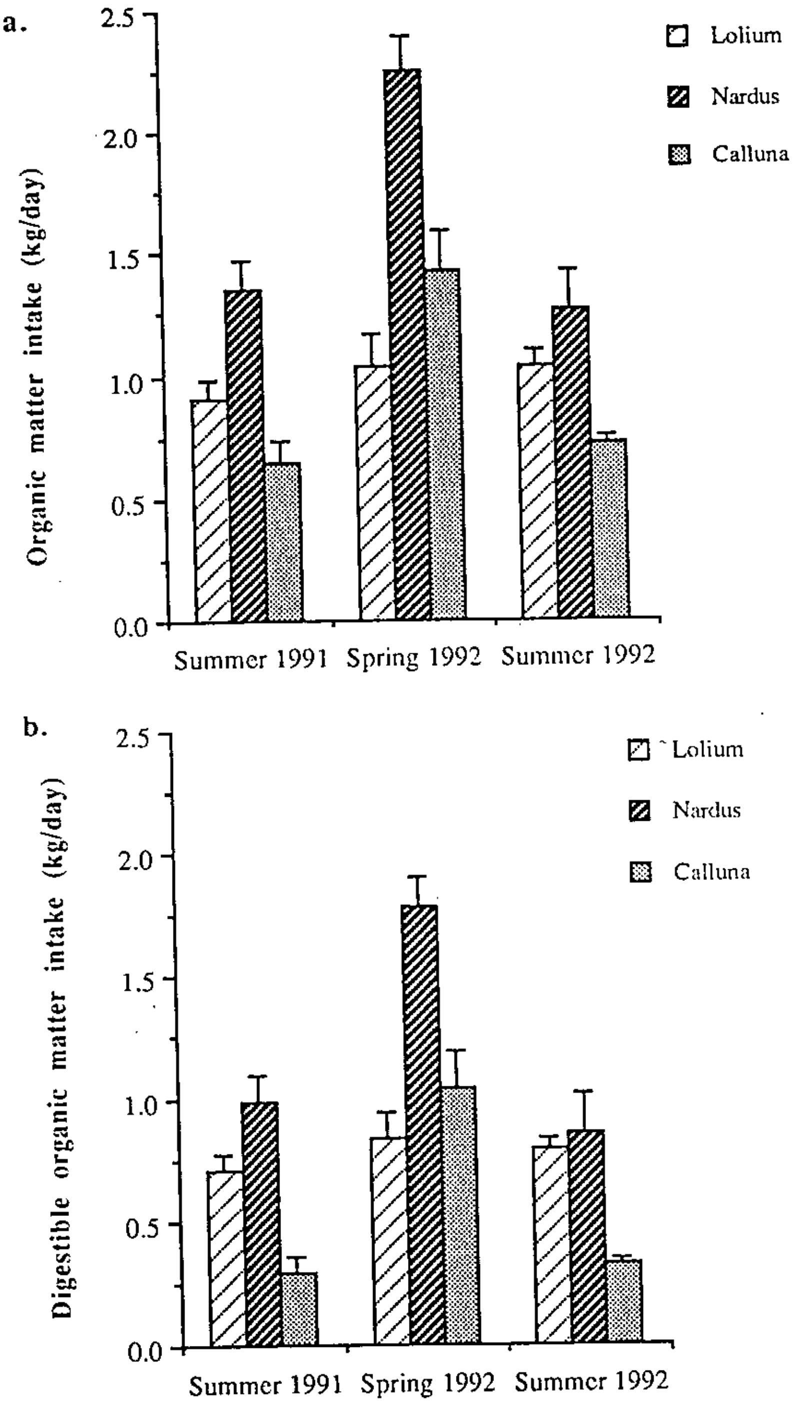


Figure 5.5: Effect of season and vegetation type on: a. organic matter intake; and b. digestible organic matter intake of goats (kg/day)

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	0.704 ± 0.0605	0.837 ± 0.1092	0.790 ± 0.0445
Nardus	0.983 ± 0.1117	1.785 ± 0.1230	0.859 ± 0.1615
Calluna	0.297 ± 0.0618	1.044 ± 0.1475	0.322 ± 0.0231

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	ns	ns	ns
Nardus	***	ns	***
Calluna	**	ns	**

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	ns	*	**
Spring 1992	***	ns	***
Summer 1992	ns	**	**

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 5.13: Digestible organic matter intake of goats (kg/day)

No significant differences were recorded between sessions in the goats' DOMI on the Lolium sward. In contrast, on both indigenous communities DOMI was higher during the spring session than either summer session.

During both summer sessions the DOMI of the goats on the grasslands communities was significantly higher than that on the dwarf-shrub community. During spring DOMI on the Nardus community was higher than that on either the Lolium or Calluna communities.

5.5 GRAZING PATTERN

5.5.1 Total grazing time

The total grazing time of the goats on each community during each experimental session are listed in Table 5.14a and plotted in Figure 5.6. Statistical differences are summarised in Table 5.14b and 5.14c.

Although there was no difference between the total grazing time of the goats on the Lolium sward in summer 1991 and that in spring 1992 there was a significant increase in summer 1992 in comparison with the spring session. No differences were found between the three grazing times recorded when the goats were selecting from the Nardus community. The results for the Calluna community indicate the goats spent significantly more time grazing in summer 1991 than either session in 1992.

During the experimental sessions in summer 1991 and spring 1992 there was a significant increase in the amount of time spent grazing when the animals were on either of the indigenous communities relative to that on the Lolium sward. In contrast, for summer 1992 there were no differences between the total grazing times recorded on the three vegetation types.

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	266 ± 20.3	270 ± 17.7	334 ± 23.0
Nardus	388 ± 21.3	374 ± 30.7	358 ± 20.2
Calluna	450 ± 21.6	349 ± 38.6	311 ± 22.1

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	ns	ns	*
Nardus	ns	ns	ns
Calluna	**	***	ns

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	***	***	ns
Spring 1992	***	*	ns
Summer 1992	ns	ns	ns

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 5.14: Total grazing time of goats (min/day).

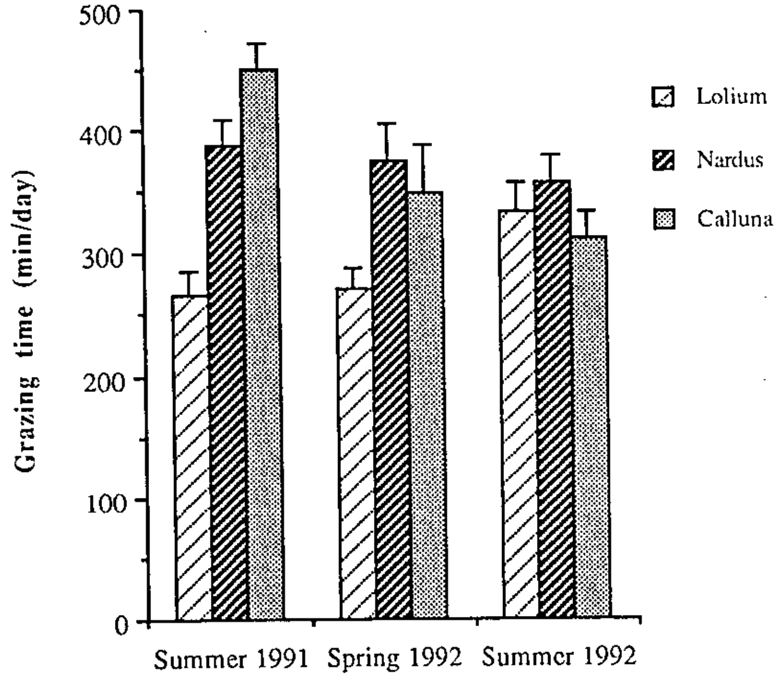


Figure 5.6: Effect of season and vegetation type on total grazing time of goats

5.5.2 Grazing pattern

The grazing pattern of the goats on each occasion was also determined from the vibracorder data. Figure 5.7 shows as an example the cumulative results for the measurement weeks in 1991, which are similar to those for both sessions in 1992. The goats grazed mainly during daylight hours, with the general pattern similar on all three vegetation types.

4.5.3 Synchronisation of grazing

The kappa coefficients of synchronisation (K) of grazing, not grazing and overall activity on each vegetation type are given in Table 5.15, together with the variance and z statistics for each K.

The z statistics calculated indicate that irrespective of vegetation type there was greater synchronisation of both grazing and not grazing amongst the group of goats than would be expected by chance. The increased coefficients of synchronisation for not grazing in comparison with those of grazing can be accounted for by the goats confining their grazing primarily to daylight hours (Figure 5.7). .

There were no seasonal change in the kappa coefficients calculated; neither was there a consistent order within sessions in the K values for overall activity calculated for each vegetation type.

5.5.4 Bite rates

The bite rates for the goats on each community during each experimental session are listed in Table 5.16a and plotted in Figure 5.8. Statistical differences are summarised in Table 5.16b and 5.16c.

Only one significant difference between sessions was recorded. The bite rate on the

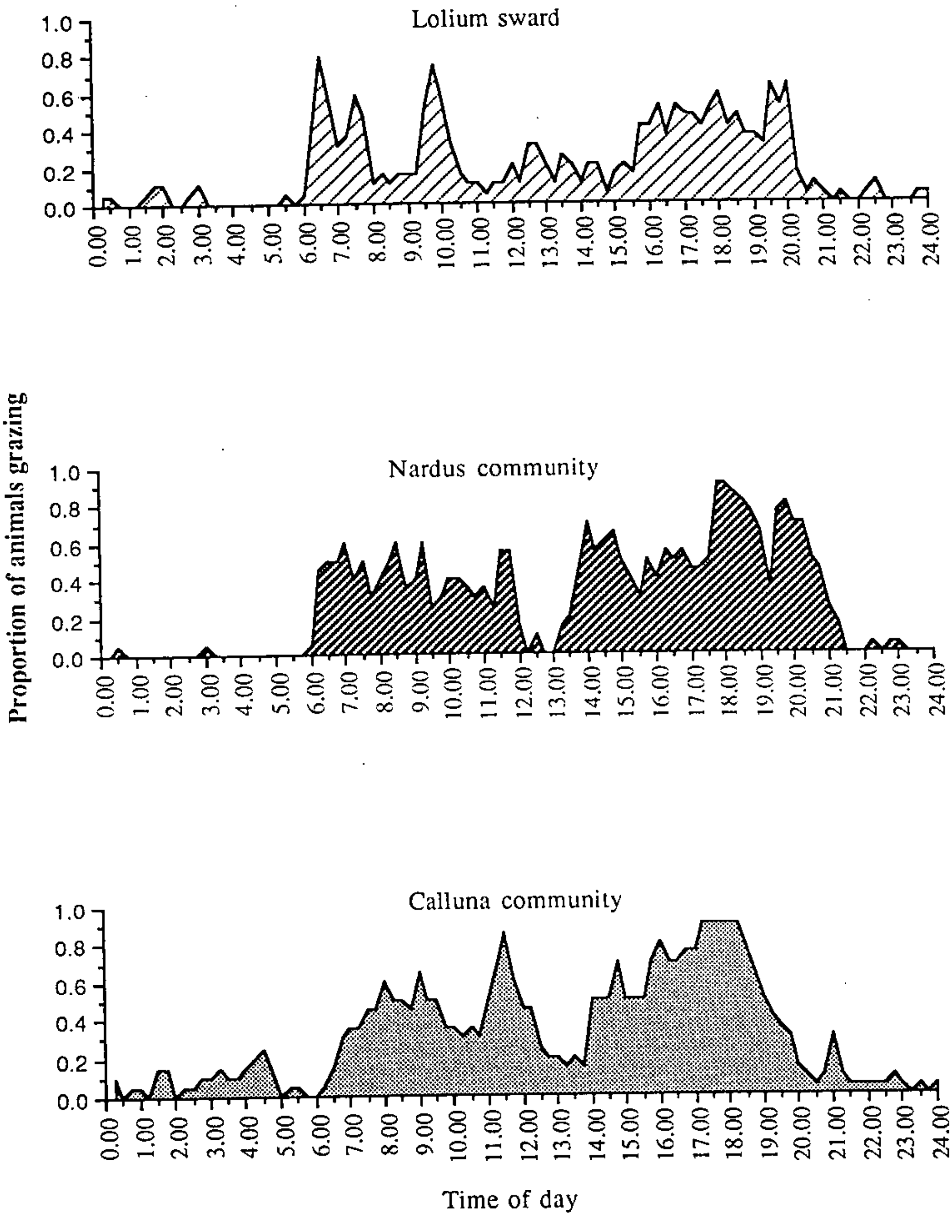


Figure 5.7: Effect of season and vegetation type on grazing pattern of goats.

		Grazing			Not grazing			Total		
Session	Vegetation	K	Var (K)	z	K	Var (K)	z	K	Var (K)	z
Summer 1991	Lolium	0.035	0.0000148	9.15	0.098	0.0018729	2.27	0.220	0.0014190	5.84
	Nardus	0.030	0.0000163	7.48	0.083	0.0019397	1.89	0.187	0.0014646	4.87
	Calluna	0.060	0.0000347	10.13	0.132	0.0015375	3.37	0.307	0.0010364	9.52
Spring 1992	Lolium	0.071	0.0000444	10.78	0.134	0.0009063	4.46	0.322	0.0005168	14.18
	Nardus	0.068	0.0000611	8.69	0.133	0.0015419	3.41	0.317	0.0009709	10.19
	Calluna	0.066	0.0000395	10.50	0.131	0.0010646	4.01	0.310	0.0006476	12.19
Summer 1992	Lolium	0.080	0.0000669	9.73	0.131	0.0007516	4.78	0.325	0.0003688	16.91
	Nardus	0.060	0.0000365	9.98	0.125	0.0012241	3.59	0.294	0.0007799	10.54
	Calluna	0.060	0.0000283	11.20	0.133	0.0013051	3.68	0.308	0.0008725	10.41

K = kappa coefficient of synchronisation
Var(K) = variance of K
z = z statistic for K

Table 5.15: Grazing synchronisation of goats

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	39.7 ± 2.94	46.5 ± 4.79	38.5 ± 3.62
Nardus	34.5 ± 3.92	46.9 ± 3.07	41.0 ± 3.07
Calluna	34.4 ± 2.56	33.4 ± 1.35	32.9 ± 2.16

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	ns	ns	ns
Nardus	*	ns	ns
Calluna	ns	ns	ns

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	ns	ns	ns
Spring 1992	ns	*	*
Summer 1992	ns	ns	ns

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites
ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$

Table 5.16: Bite rates of goats (bites/min).

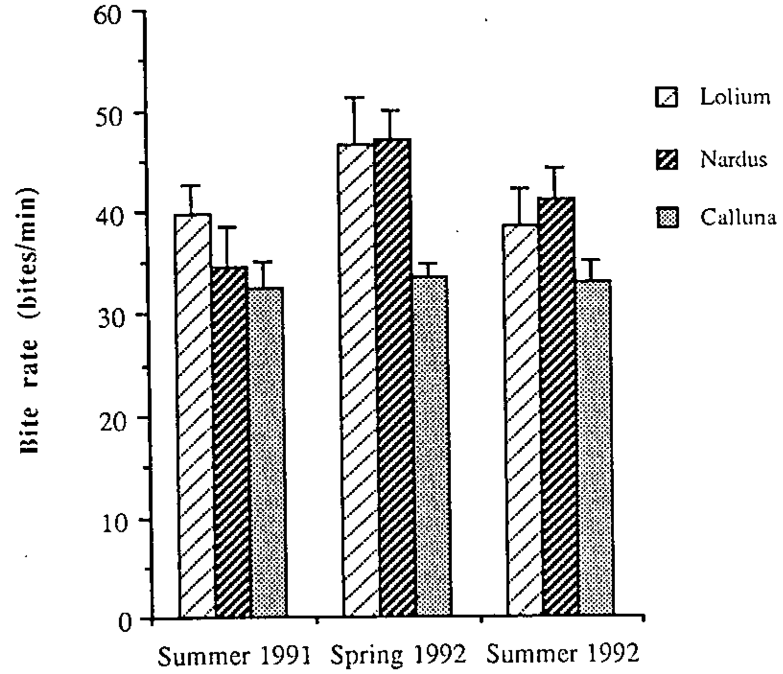


Figure 5.8: Effect of season and vegetation type on bite rates of goats

Nardus community in summer 1991 was found to be lower than that in spring 1992.

During summer 1991 no significant differences between bite rates on the three vegetation communities were recorded. In spring 1992 the bite rate on the Calluna community was recorded as being lower than that on either grassland community. However, during the summer 1992 session the bite rates on all three vegetation communities were again similar.

5.6 DISCUSSION

Previous studies of goats on similar vegetation types to those grazed during the current trial have concentrated on the effect of the animal on vegetation dynamics and/or focused on the utilisation of a particular plant species (e.g. Russel *et al.*, 1983; Grant, Bolton and Russel, 1984; Bullock and Kinnear, 1988; Merchant, 1993; Smith and Bullock, 1993). Consequently only limited interpretation of the results of these studies has been possible. In addition there are surprisingly few comparable results regarding diet composition, diet digestibility and intake of free-roaming goats on temperate vegetation communities are available.

The overall response of the goats to the sown sward was markedly different to their reaction to the two indigenous communities. On the Lolium sward the goats were generally inconsistent in their selection for and against the various vegetation categories available in the sward. Thus, although the proportion of the diet accounted for by dicotyledonous plants in summer 1991 was lower than the proportion recorded in the sward during the same session, during both experimental periods in 1992 the proportions in the diet and sward were similar. Likewise during all three experimental sessions the ratio of *Trifolium repens* to other dicotyledonous plants in the diet of the goats matched that in the sward.

The low incidence of dead lamina of broad-leaved grasses together with the general avoidance of grass vegetative stem indicates that the goats were confining their grazing to the upper strata of the sward. A study of dietary overlap between sheep, cattle and goats grazing in common showed that similarity was greatest between goats and cattle (Squires, 1982), and cattle are known to graze at shallower depths within the sward canopy than sheep (Hodgson and Grant, 1981). Grant, Bolton and Russel (1984) also concluded that differences in utilisation of grass and clover by sheep and goats reflected a difference in grazing height. Thus the goats exhibited stronger vertical than horizontal selection within the sward and the impression is of relatively indiscriminate consumption of material at or near the sward surface.

In contrast on both indigenous communities the goats were found to be more discerning in the diet they selected from the range of plant species and plant parts available. In the case of the Nardus dominated grassland pronounced seasonal changes in dietary composition were also identified. During the spring session there was no longer avoidance of *Nardus stricta* green lamina while the strength of selection of broad-leaved grasses was reduced and there was a switch to consumption of *Luzula* spp.. This tolerance of *Nardus stricta* extends only to green leaves and corresponds to an increase in the digestibility relative to green lamina of the mature plants encountered during the summer experimental sessions (see Chapter Four).

Although the digestibility of green lamina of the broad-leaved species of grass was also higher during the spring session, the proportion of the total sward accounted for by this category was at its lowest and the proportion in the diet was approximately half that recorded during the summer sessions. However, as the proportion of *Luzula* spp. leaves in the sward was lower, the switch to strong selection for this genera in the spring must be related to a factor or factors other than availability. Unfortunately, the contribution of this category to the sward profile during the spring experimental session was so small that insufficient material was accumulated during the botanical separations of the herbage side-clips to allow an *in vitro* determination to be performed. Consequently it was not possible to establish whether a change in digestibility of this genera would account for the goats' strong selection in spring. Similar preferences for other plant categories have been noted with, for example, consumption of *Juncus* spp. being recorded at a time when grasses of higher digestibility were available (Bullock, 1985). Such preferences can be exploited as an effective management tool to eliminate or control such plant species in sheep pasture (Merchant, 1993), although if high stocking densities are used there is a risk of associated liveweight loss leading to animals of poor condition vulnerable to parasite infection and cold stress (McGregor, 1985).

Regardless of the factor or factors bringing about this seasonal switch in selection for *Luzula* spp., the implications of strongly selecting for this type of vegetation category are worthy of comment. It was noted in the field that the *Luzula* spp. patches being consumed by the goats occurred in distinct patches, and this is verified by the Green's Index value calculated from the point quadrat data. Thus, although material was observed as being consumed en route between patches, by concentrating on the clumps of *Luzula* spp. the goats will have limited the range of additional plant species they encountered. In addition, since individuals tended to graze in relatively close proximity selection for comparatively small patches of vegetation led to competition for the same resource and aggression being observed.

This seasonal change in diet composition on the indigenous grassland community was complemented by a seasonal change in organic matter intake. Whereas there were no significant differences between the organic matter intakes of the goats in spring and summer on the sown sward, on the Nardus community intake was recorded as being significantly higher during the spring experimental session. However, the overall digestibility of the diet selected at this time was not significantly different to the digestibility of the diets consumed during either summer session. A possible explanation is that bite selection was relatively more time-consuming during the summer sessions when the switch from vegetative to reproductive growth of most of the plant species available will have reduced the overall digestibility of the sward. Thus although diet digestibility was maintained once again it was at the expense of organic matter intake since grazing time was unaltered. Similar results have been reported for goats grazing lightly and heavily stocked ranges (Malechek and Leinweber, 1972a). Alternatively the higher intake recorded in spring could have been due to increased palatability of particular food items available at that time relative to those encountered during the summer sessions. This would be in keeping with the switch to strong selection for *Luzula* spp..

A seasonal change in organic matter intake was also recorded on the dwarf-shrub community. Thus the goats were apparently unable to sustain the spring value for diet digestibility later in the season when the proportions of green leaves of graminoid species and *Vaccinium* spp. were lower, despite sacrificing daily intake. Indeed there are indications of another seasonal switch in diet composition, albeit of reduced magnitude in comparison to that exhibited on the Nardus grassland, with elevated proportions of grass vegetative stem, flowerstem and seed/flowerhead being recorded in the spring diet. Similar variations in the consumption of perennial grasses and an associated effect on the amount of browse selected have been recorded among goats on rangeland (Malechek and Leinweber, 1972b; Bryant, Kothmann and Merrill, 1980). However, goats have also been recorded as preferentially consuming *Calluna vulgaris* (Bullock, 1985) and apparent avoidance of graminoids in a tree/shrub dominated habitat has also been observed (Smith and Bullock, 1993). Thus it would appear that, despite the emphasis in the literature on the contribution of shrubs and trees to the diets of goats, they cannot be classified as obligatory browsers. Instead their consumption of grass and/or browse depends on the specific opportunities available. The variability of the goats diet suggests that this species will quickly adapt its grazing strategy to accommodate specific opportunities available. However, further research is required to identify the additional factors which contributed to the substantial between-animal and within-animal differences in diet composition of the goats which were recorded. This unpredictability, together with their selection of ephemeral plant species suggest that grazing by goats would be undesirable in conservation areas where rare plant species are found.

As previously indicated, the goats confined their grazing to the upper strata of the Lolium sward and similar findings have been reported elsewhere (Grant, Bolton and Russel, 1984). However, the inclusion of some moss and the selection of grass vegetative stem in spring on the Calluna community indicate that the goats were prepared to select items from the base of the this community. This is despite the nature of the architecture of the dominant plant species restricting access to the base layer, and illustrates the advantages of mobile lips and narrow mouths in selecting particular food items.

The differences in diet digestibility and intake were not reflected in differences in total grazing time. In general the grazing times recorded during this study were lower than those estimated by observation on Texas rangeland (Askins and Turner, 1972) and on hill vegetation in Spain (K. Osoro, *pers. com.*).

During the microscopic examinations of the extrusa samples it was noted that fragments of vegetation in the material collected by the goats were smaller and more damaged than those in the samples from the red deer or camelids. This suggests prehended material was being chewed more thoroughly prior to swallowing which is consistent with results of comparisons with sheep (Domingue, Dellow and Barry, 1991a). Increased chewing will result in a greater proportion of particles which can be classed as small or intermediate in size entering the rumen (Domingue, Dellow and Barry, 1991a). In addition large particles which have resisted breakdown in the mouth will be structurally weakened increasing the chance of these fracturing directly into small particles, without passing through an intermediate size. Even though more fibrous material such as flowerstem will not be broken down to the same degree by chewing as green lamina, smaller particles relative to those produced by the other two species of animal could result. Animals of small body size, such as goats, are unable to retain fibrous particles for microbial degradation for as long without an unacceptable reduction in intake (Campling, 1964). By decreasing particle size the surface area of particles which is available for microbial attachment and colonisation will be increased (Elliot and Norton, 1985; Domingue, Dellow and Barry, 1991b). In addition transit time will be decreased (Poppi *et al.*, 1980; Lechner-Doll, Kask and Engelhardt, 1991) creating an opportunity to increase voluntary food intake (Domingue, Dellow and Barry, 1991b). Thus digestibility of a given feed consumed *ad libitum* may be lower, but total consumption of digestible material could be increased. In such circumstances a high throughput of material could result in an increase in intake on poorer quality vegetation. This would account for the higher organic matter intakes on the indigenous grassland in comparison with the sown sward. On the dwarf-shrub community where differences in digestibility between plant species and plant parts were more extreme maintaining selective feeding would be of primary importance even if this was at the expense of organic matter intake.

Smaller particles will pass quickly from the rumen having undergone comparatively limited microbial digestion. Thus such a system would also be advantageous where an animal could consume high quality food items which did not require preliminary fermentation since it would minimise unnecessary energy loss to the microbial population (Demment and Greenwood, 1988). Under these circumstances the animal would be expected to select a diet comparatively high in water soluble carbohydrates and low in structural carbohydrates, and exploit variations in the susceptibility of different food items to breakdown during chewing. This may go some way to explain the variability of diet selection by the goats and the associated exploitation of plant species at particular stages of growth recorded here and elsewhere (Genin and Badan-Dangon, 1991; Fedele *et al.*, 1993).

5.7 SUMMARY

1. Goats were found to be flexible in their dietary habits, but were also highly selective, particularly on the indigenous communities.

2. When grazing on the Lolium sward the goats exhibited selection for green leaf at or near the sward surface, regardless of plant species. In contrast, on the indigenous communities there was discrimination between different plant genera and species, in addition to selection of green and avoidance of dead material.

3. On the Nardus community the goats avoided the dominant tussock-grass, with the degree of avoidance increasing in summer. Broad-leaved grasses from the inter-tussock areas were strongly selected, and were the main dietary component. Minor components from within the sward were also consumed in varying amounts. In particular, non-grass monocotyledonous plants made a substantial contribution to the spring diet.

4. On the Calluna community, *Calluna vulgaris* was avoided whereas *Vaccinium* spp. and graminoid species were selected.

5. Diet digestibility was strongly influenced by vegetation type. OMI was also influenced by vegetation type, and on the indigenous grassland was also affected by season. Differences in DOMI between sessions and between vegetation types within sessions reflected the pattern of differences in OMI, indicating that diet digestibility varied less than intake.

6. The goats grazed mainly during daylight hours. Neither vegetation type nor season had a consistent effect on total grazing time or bite rate.

CHAPTER SIX

DIET COMPOSITION AND INGESTIVE BEHAVIOUR OF RED DEER

6.1 REVIEW

The deer family are placed within the Order Artiodactyla (even-toed ungulates), suborder Ruminantia, Infraorder Pecora. The living Pecora comprises, in addition to the Cervidae, the families Moschidae (musk-deer) Giraffidae (giraffes and okapi); Bovidae (cattle, antelopes, etc.) and Antilocapridae (pronghorns). The Cervidae comprise forty species from seventeen genera, some of the species appearing totally unalike in size, behaviour, performance and especially in their feeding and digestive strategies (Hofmann 1985). This diversity and the evolutionary lineages of the Cervidae reflect their responses to selective forces including predators, pathogens and the processes of resource partitioning and niche selection (Harrington, 1985).

Red deer are indigenous between latitudes 30° and 65° in the Northern temperate zone (Mitchell, Staines and Welch, 1977) with a wide but discontinuous distribution. It has been suggested that the species' current flexibility originated in response to the environmental fluctuations to which it was exposed during the Middle and Upper Pleistocene (Lister, 1984) and that a high degree of genetic variation is maintained, helping the species persist in a variable habitat (Harrington, 1985). Certainly, throughout their natural range red deer are found in a variety of climatic and vegetation types, although they have a preference for areas which provide cover (Lockie, 1967; Staines and Welch, 1984) and are encountered most characteristically in upland forest or woodland areas with locally open spaces (Lister, 1984). Kay and Staines (1981) provide an extensive review of the range and habitat types of wild deer highlighting this versatility and commenting on the resultant variation in performance.

Within the areas of Europe which support an indigenous population of red deer body weight and antler size increase progressively from north-west to south-east. Thus those in Hungary, Yugoslavia and Bulgaria have around 2 to 2.5 times the body weight and around 3 to 4 times the antler weight of those on Scottish hill-land (Mitchell, Staines and

Welch, 1977). Such differences are largely due to the effects of environment and nutrition, and Lowe (1961) has reviewed the multiple factors which can be implicated in the dramatic decrease in size of red deer since their arrival in Scotland at the end of the Pleistocene. Within the red deer population in Britain there are further variations in size, with those on hill pastures achieving adult liveweights which are generally substantially lower than those in afforested areas (Ratcliffe, 1987) and those of farmed red deer (Loudon and Hamilton 1989). Hill pastures and associated restrictions in winter forage quality have an allied role in limiting body weight and ultimate population size .

Red deer have been important to man since pre-historic times and have been kept in parks and enclosed forest land in Europe for at least five centuries. However, it is only recently that they have been farmed along the same lines as other domestic livestock (Louden and Hamilton, 1989). In general the increased pressures from afforestation, agriculture and recreation have resulted in deer being restricted to the poorer-quality, more remote and exposed hill-land. In Scotland the majority of deer are free-ranging passing from one estate to another and are simultaneously considered pests and commercially viable.

Volatile fatty acids within the rumens of red deer are apparently produced and removed in similar patterns to those of sheep (Maloiy, Kay and Goodall, 1968; Prins and Geelen, 1971; Hobson *et al.*, 1976) with similar factors governing concentrations and activities of microbes in the alimentary tract. For example, rumen bacterial and protozoal counts of red deer have been found to vary with season and appear to reflect differences in nutritional state (Hobson, Mann and Summers, 1976).

Red deer undergo conspicuous cycles of reproductive activity and moulting which are entrained by photoperiod (Mitchell, McCowan and Nicholson, 1976), and exhibit related seasonal trends in voluntary food intake (Suttie and Simpson, 1985) and body condition

(Mitchell, McCowan and Nicholson, 1976). Consequently intake is lower in winter and higher in summer when there are demands for growth, lactation and storing fat for the rut and for winter. As this increased voluntary food intake is not associated with a depression in digestibility (Milne *et al.*, 1978; Barry *et al.*, 1991) or mean retention time (Milne *et al.*, 1978), it has been suggested that there may be a compensatory enlargement of the digestive tract (Milne *et al.*, 1978) allowing digestive efficiency to be preserved despite major seasonal changes in voluntary food intake. Certainly large increases in rumen pool size of both liquid and solid digesta have been demonstrated (Domingue *et al.*, 1991; Barry *et al.*, 1991) in summer compared with winter. However, more recent findings suggest that the extra digesta load is not accommodated by hypertrophy of any part of the alimentary tract but by an increase both in the dry matter content of the digesta and in the degree of rumen fill (Sibbald and Milne, 1993).

Although work has shown that red deer digest fibrous diets less well than sheep and that this is associated with a more rapid passage of food through the digestive tract (Kay and Goodall, 1976), Milne (1980) concluded that differences in digestibility and mean retention time at equal intakes for red deer and sheep are unlikely to be large on higher quality diets.

Like goats, red deer are intermediate feeders under Hofmann's (1973) classification and they share a number of other features. A wide variety of food species are consumed and much of the variation in diets can be related to differences in plant availability (Kay and Staines, 1981; Jenkins and Starkey, 1991). It has been suggested that by selecting a great number of different plants the toxic effects of certain plants is reduced while their nutritive value is exploited (Hofmann, 1985). They are seasonally and regionally adaptable taking browse and grasses in various amounts according to season and area. Thus, while grass has been found to be the most important dietary component in summer the contribution of heather increases in winter (Jensen, 1968; Hobson *et al.*, 1976).

Similarly heather has been recorded as being ingested in different amounts according to area apparently irrespective of the amount on offer, which may relate to site characteristics, or the presence of other more or less palatable species (Charles, McCowan and East, 1977).

Despite the number of studies on interactions between deer and their natural ecosystems, little work has been done giving an insight into food selection at a detailed level, either in relation to the quality of plant species or the actual mechanisms of selection. While selection of plant communities has been investigated using observations and/or faecal counts (Charles, McCowan and East, 1977; Gordon, 1989b), selection of individual plants or plant parts has tended to rely on visual assessment of removal of vegetative matter, particularly from shrubs and trees (e.g. Kossak, 1976), examination of rumen contents (e.g. Jensen, 1968; Prins and Geelen, 1971; Hobson *et al.*, 1976), or analysis of faecal material. More controlled experiments have often involved only one or two animals making interpretation limited (e.g. Staines, 1968; Maloiy, Kay and Goodall, 1968; Dzieciolowski, 1970; Yalden 1978).

RESULTS

6.2 DIET COMPOSITION

Variations in the proportions of a given component in the diet attributable to plot effects or plot x session interactions were rare (Tables 6.2, 6.5 and 6.8) indicating the composition of the diets selected by the deer during each experimental session were consistent.

6.2.1 The Lolium sward

The mean proportions of components in the diet selected by the red deer from the sown sward on each occasion are tabulated and depicted in Table 6.1 and Figure 6.1 respectively.

Vegetation category			**Summer 1991**	**Spring 1992**	**Summer 1992**
broad-leaved grasses	leaf	green	90.0 ± 1.25	65.9 ± 3.35	63.4 ± 3.74
		dead	1.4 ± 0.48	4.3 ± 1.11	4.6 ± 0.81
grass vegetative stem			1.7 ± 0.47	1.9 ± 0.54	0.9 ± 0.30
grass flowerstem			0.8 ± 0.29	1.8 ± 0.42	1.0 ± 0.55
grass seed/flowerhead			0.9 ± 0.19	3.0 ± 0.89	0.3 ± 0.20
Trifolium repens	leaf	green	4.8 ± 1.30	8.4 ± 2.04	19.1 ± 4.32
		dead	0.2 ± 0.05	0	0.2 ± 0.14
	petiole		0	0.5 ± 0.36	0.7 ± 0.20
	flower		-	0.1 ± 0.09	0
other dicots	leaf	green	0.1 ± 0.00	13.3 ± 3.87	9.6 ± 2.75
		dead	0	0.3 ± 0.13	0.2 ± 0.10
	stem		0	0.3 ± 0.16	0
	flower		-	0.1 ± 0.12	-
moss			0.1 ± 0.12	-	-
			n = 9	n = 11	n = 12

0 = recorded in vegetation but not in diet. - = absent from vegetation and diet.

All results expressed as mean percentage ± s.e.m.

Table 6.1: Composition of the diets consumed by the red deer on the Lolium community.

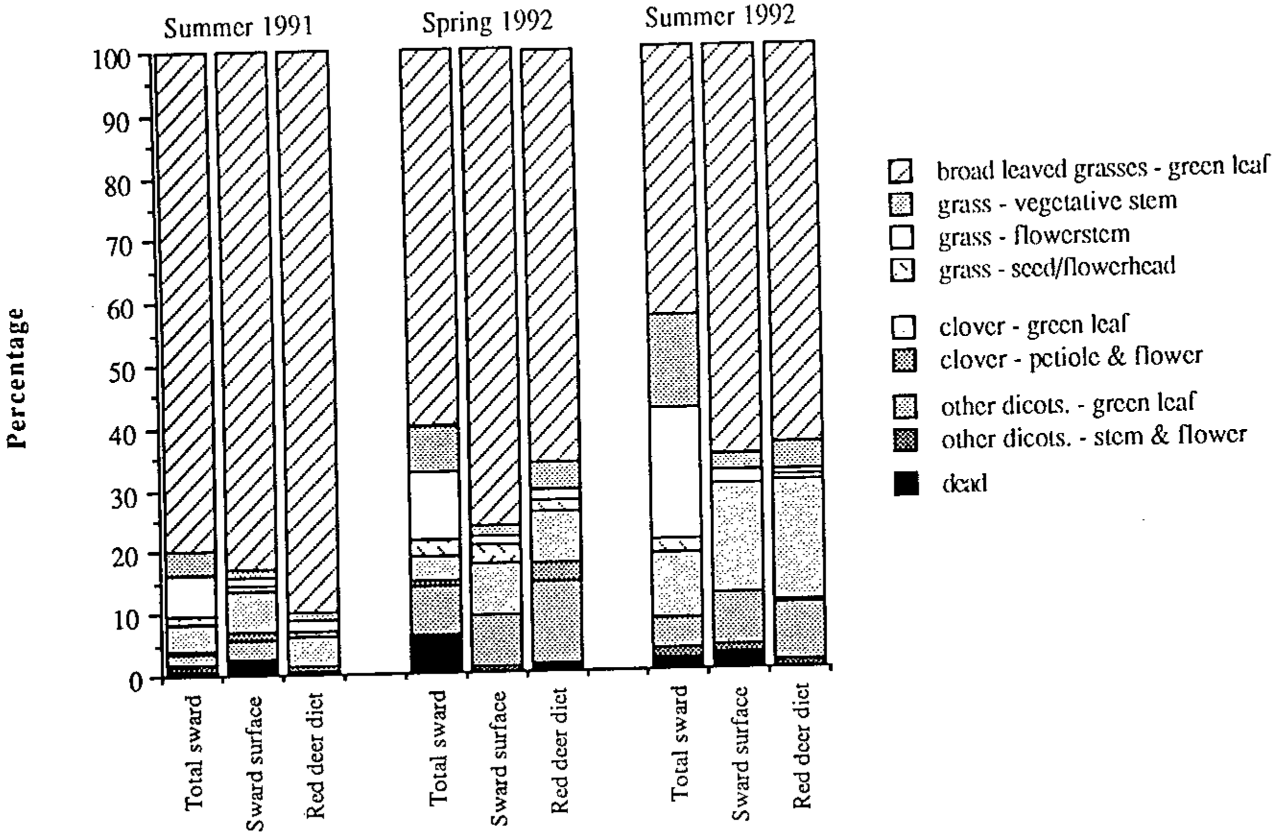


Figure 6.1: Composition of the diets consumed by the red deer on the Lolium sward.

Green lamina of the broad-leaved grasses was the main component in the diet selected on each occasion; accounting for between 60 and 90 per cent of the material consumed. In contrast, the amount of dead lamina never exceeded 5 per cent and the remaining morphological units of grass each contributed less than a total of 3 per cent. The significantly lower proportion of green lamina in the diets selected during the experimental sessions in 1992 (Table 6.2) corresponded to an increase in the amount of dicotyledonous plants consumed. Once again green leaves of dicotyledonous plants made the principal contribution to the diet whereas the amounts of dead leaves, stem and flowers recorded were negligible.

The Electivity Index values for the components in the diets selected from the Lolium sward are summarised in Table 6.3. While weak selection for green lamina of broad-leaved grasses and for grass seed/flowerhead was identified, dead lamina, vegetative stem and flowerstem were avoided in comparison with the proportions of these components in the sward as a whole. Selection for or against of the grass categories in comparison with the proportions recorded at the sward surface was more variable. Similarly there was no clear pattern in the selection index values for the different morphological units of clover or other dicotyledonous plants.

6.2.2 The Nardus community

The mean proportions of components in the diet selected from the *Nardus stricta* dominated community on each occasion are tabulated and depicted in Table 6.4 and Figure 6.2 respectively.

The dominant tussock-grass of the indigenous grassland was avoided by the red deer. Instead they selected their diets from the relatively species-rich inter-tussock areas. Green lamina of broad-leaved grasses was identified as the main dietary component and consistently accounted for over sixty per cent of the material consumed. A significantly

Vegetation category			Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992	
broad-leaved grasses	leaf	green	**	***	ns	
		dead	*	*	ns	
grass vegetative stem			ns	ns	ns	ψ
grass flowerstem			ns	ns	ns	
grass seed/flowerhead			*	ns	***	
Trifolium repens	leaf	green	ns	**	**	
		dead	ns	ns	ns	
	petiole		ns	**	ns	
other dicots	leaf	green	***	***	ns	
		dead	*	ns	ns	
	stem		*	ns	*	
	flower		ns	ns	ns	
moss			ns	ns	ns	

ns = not significant; * = p<0.05; ** = p<0.01; *** = p<0.001
ϕ = plot effect
ψ = plot x session interaction

Table 6.2: Summary of statistical analysis comparing the diets selected by the red deer from the Lolium sward during each experimental session

			Summer 1991		Spring 1992		Summer 1992	
Vegetation category			**Total**	**Surface**	**Total**	**Surface**	**Total**	**Surface**
broad-leaved grasses	leaf	green	+	+	+	-	+	0
		dead	- -	-	-	+ +	- -	+
grass vegetative stem			- -	+	- -	0	- -	-
grass flowerstem			-	-	-	0	-	-
grass seed/flowerhead			+	0	+ +	0	+ +	+ +
Trifolium repens	leaf	green	0	-	+	0	+	0
		dead	-	+ +	- -		-	+ +
	petiole		- -	- -	+ +	+ +	-	+ +
	flower				+ +	+ +	- -	
other dicots	leaf	green	- -	- -	+	+	+	0
		dead	- -		- -	+ +	-	+ +
	stem		- -	- -	- -	-	- -	- -
	flower				0	- -		
moss			+ +	+ +				

Abbreviations: + + = strong selection; + = weak selection; 0 = indifference; - = weak avoidance; - - = strong avoidance; blank = absent from vegetation and diet.
Total = relative to proportion in total sward. Surface = relative to proportion at sward surface.

Table 6.3: Selectivity indices for red deer diets from the Lolium sward.

Vegetation category			Summer 1991	Spring 1992	Summer 1992
Nardus	leaf	green	1.1 ± 0.30	1.9 ± 0.75	0.8 ± 0.27
		dead	0.4 ± 0.15	0.3 ± 0.18	0.1 ± 0.07
broad-leaved grasses	leaf	green	76.2 ± 2.63	61.3 ± 1.85	69.4 ± 2.73
		dead	3.7 ± 0.85	16.6 ± 1.99	12.1 ± 0.81
Festuca	leaf	green	2.4 ± 0.66	0.8 ± 0.19	0.8 ± 0.41
		dead	0.4 ± 0.26	0.3 ± 0.11	0.3 ± 0.14
Deschampsia	leaf	green	4.5 ± 0.81	6.9 ± 1.08	7.9 ± 1.40
		dead	0.1 ± 0.08	1.7 ± 0.46	0.8 ± 0.25
grass vegetative stem			2.6 ± 0.12	4.1 ± 0.62	4.3 ± 0.06
grass flowerstem			3.5 ± 0.54	3.5 ± 0.77	1.8 ± 0.65
grass seed/flowerhead			1.8 ± 0.70	0.9 ± 0.82	1.0 ± 0.29
Carex	all	green	0	0	0
		dead	-	0	-
Luzula	flower		-	0.1 ± 0.07	-
	leaf	green	0.2 ± 0.18	0	0.1 ± 0.04
		dead	0	0	0.1 ± 0.08
other monocots.	all	green	0	-	0
		dead	0	-	0
Galium	all	green	1.3 ± 0.55	0.1 ± 0.13	0.5 ± 0.29
		dead	0	-	0
Vaccinium	all	green	0.4 ± 0.26	0.3 ± 0.27	0
		dead	0	-	0
Potentilla	all	green	1.3 ± 0.73	0	0
		dead	0	0	-
other dicots.	all	green	0	-	-
moss			0.2 ± 0.51	1.1 ± 0.47	0.1 ± 0.23

0 = recorded in vegetation but not in diet. - = absent from vegetation and diet.
All results expressed as mean percentage ± s.e.m.

Table 6.4: Composition of the diets consumed by the red deer on the Nardus community.

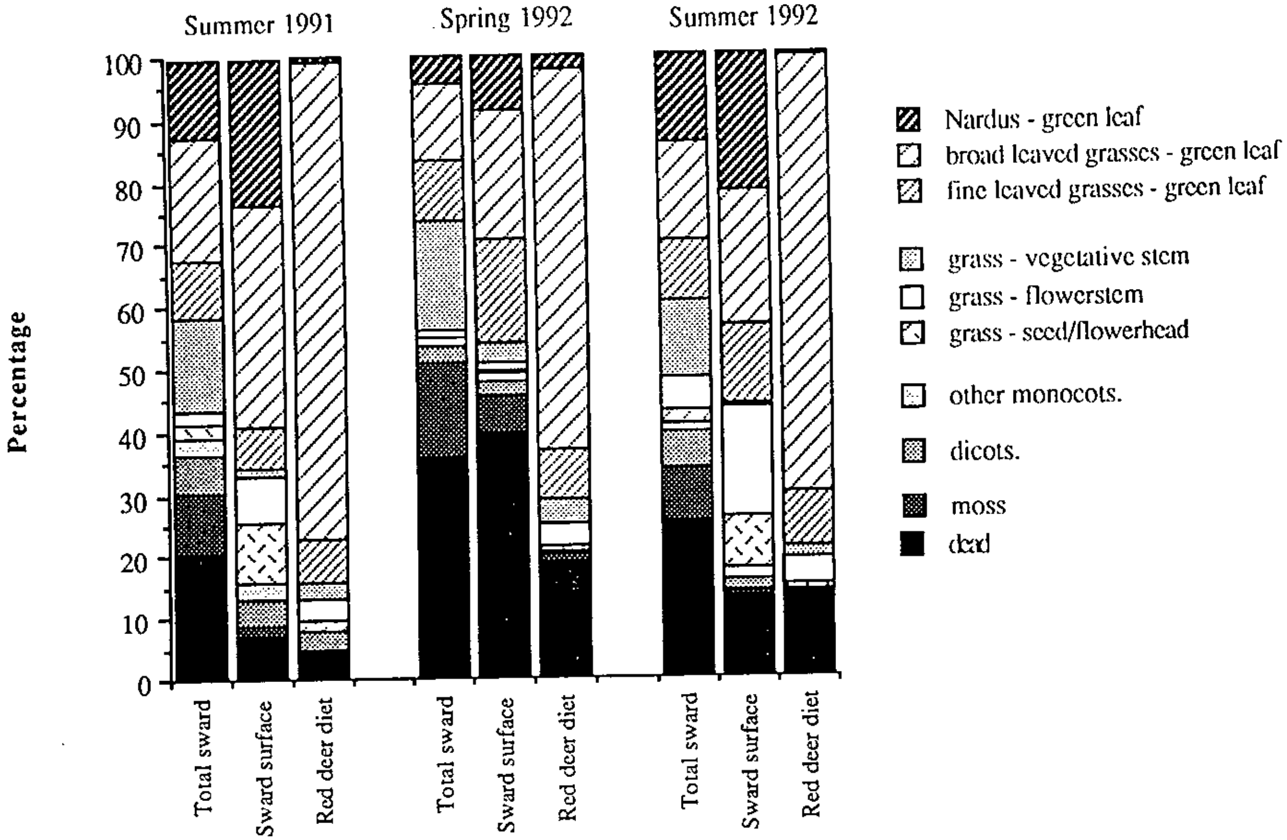


Figure 6.2: Composition of the diets consumed on the Nardus community by the red deer.

lower proportion of this component during the 1992 experimental sessions (Table 6.5) corresponded with a significantly greater proportion of the diet accounted for by dead lamina of these grasses. Of the two species of fine-leaved grasses found in the inter-tussock areas *Deschampsia flexuosa* made the greater contribution.

Levels of the other morphological units of grass in the diets consumed on each occasion were low. Similarly the grass-like monocotyledonous plants and dicotyledonous plants made little contribution to the diets consumed by the deer.

The Electivity Index values for the components identified in the diets consumed by the red deer on the Nardus community are listed in Table 6.6. In general there was strong avoidance of lamina of *Nardus stricta* and *Festuca ovina*. In contrast there was strong selection for lamina of broad-leaved grasses and inconsistent selection for lamina of *Deschampsia flexuosa*. Although vegetative stem was strongly avoided in comparison with the proportion of this component in the sward as a whole, selection occurred relative to the availability of this component at the sward surface. There is an indication of a seasonal change in selectivity of flowerstem and seed/flowerhead, with these components being avoided during the summer sessions but selected in spring 1992. There was also selection of *Luzula* spp. flowers in spring 1992, but apart from this particular plant part the grass-like monocotyledonous plants were strongly avoided. The only dicotyledonous species selected was *Vaccinium myrtillus*.

6.2.3 The Calluna community

The mean proportions of components in the diet selected by the red deer from the Calluna community on each occasion are tabulated and depicted in Table 6.7 and Figure 6.3 respectively.

Two vegetation categories, green *Calluna vulgaris* shoots and green lamina of *Festuca*

Vegetation category			**Summer 1991 v. Spring 1992**	**Summer 1991 v. Summer 1992**	**Spring 1992 v. Summer 1992**	
Nardus	leaf	green	ns	ns	ns	
		dead	ns	ns	ns	
broad-leaved grasses	leaf	green	***	**	ns	
		dead	***	***	ns	ϕ
Festuca	leaf	green	ns	ns	ns	
		dead	ns	ns	ns	
Deschampsia	leaf	green	ns	ns	ns	
		dead	*	ns	ns	
grass vegetative stem			ns	ns	ns	
grass flowerstem			ns	*	*	
grass seed/flowerhead			*	ns	ns	
Luzula	flower		*	ns	*	
	leaf	green	ns	ns	ns	
		dead	ns	ns	ns	
Galium	all	green	**	*	ns	
		dead	ns	ns	ns	ψ
Vaccinium	all	green	ns	ns	ns	
Potentilla	all	green	***	***	ns	
moss			ns	ns	ns	ϕψ

ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$
ϕ = plot effect
ψ = plot x session interaction

Table 6.5: Summary of statistical analysis comparing the diets selected by the red deer from the Nardus community during each experimental session.

			Summer 1991		Spring 1992		Summer 1992	
Vegetation category			**Total**	**Surface**	**Total**	**Surface**	**Total**	**Surface**
Nardus	leaf	green	- -	- -	-	- -	- -	- -
		dead	- -	- -	- -	- -	- -	- -
broad-leaved grasses	leaf	green	+ +	+ +	+ +	+ +	+ +	+ +
		dead	-	+ +	+ +	+ +	+ +	+ +
Festuca	leaf	green	-	-	- -	- -	- -	- -
		dead	- -	+ +	- -	- -	- -	- -
Deschampsia	leaf	green	+	+	+	0	+ +	+ +
		dead	- -	-	+	+	+	+ +
grass vegetative stem			- -	+	- -	+	- -	+ +
grass flowerstem			+	-	+ +	+	- -	- -
grass seed/flowerhead			-	- -	+ +	+	-	- -
Carex	all	green	- -		- -	- -	- -	- -
		dead			- -	- -		
Luzula	flower				+ +	+ +		
	leaf	green	- -	- -	- -	- -	- -	- -
		dead	- -		- -	- -	- -	-
other monocots.	all	green	- -				- -	
		dead	- -				- -	
Galium	all	grean	- -	-	- -	- -	- -	-
		dead	- -	- -			- -	
Vaccinium	all	green	+	+	+	+ +	- -	
		dead	- -				- -	
Potentilla	all	green	0	-	- -	- -	- -	- -
		dead	- -		- -			
other dicots.	all	green	- -					
moss			- -	- -	- -	- -	- -	- -

Abbreviations: + + = strong selection; + = weak selection; 0 = indifference; - = weak avoidance; - - = strong avoidance; blank = absent from vegetation and diet.
Total = relative to proportion in total sward. Surface = relative to proportion at sward surface.

Table 6.6: Selectivity indices for red deer diets from the Nardus community.

Vegetation category			Summer 1991	Spring 1992	Summer 1992
Calluna	shoot	green	34.3 ± 4.26	14.6 ± 3.67	53.4 ± 5.04
		dead	3.2 ± 0.47	2.5 ± 0.78	6.0 ± 1.22
	wood		1.7 ± 0.49	0.5 ± 0.29	4.7 ± 0.72
	flower		2.7 ± 0.75	0.0 ± 0.03	12.1 ± 2.01
Erica	shoot	green	0.4 ± 0.39	0.4 ± 0.24	0.1 ± 0.10
		dead	0.0 ± 0.03	-	0.2 ± 0.07
	wood		0.1 ± 0.07	-	0
	flower		0	-	-
Empetrum			0	0	0
V. myrtillus	leaf	green	1.3 ± 0.46	11.2 ± 2.74	0.8 ± 0.28
		dead	1.4 ± 0.33	5.1 ± 1.67	1.0 ± 0.32
V. vitis-idaea	leaf	green	0	0	0
		dead	0	-	0
Vaccinium	stem	green	3.1 ± 0.77	1.9 ± 0.51	0.7 ± 0.18
		dead	0.2 ± 0.19	0.3 ± 0.18	0
Festuca	leaf	green	31.6 ± 2.81	50.2 ± 5.10	14.3 ± 4.95
		dead	14.1 ± 2.08	6.4 ± 1.08	5.1 ± 1.63
Deschampsia	leaf	green	0.2 ± 0.15	0	0
		dead	0.0 ± 0.03	0	0
broad-leaved grass	leaf	green	3.8 ± 1.97	1.0 ± 0.58	0.8 ± 0.24
		dead	1.2 ± 0.42	0.3 ± 0.10	0.5 ± 0.17
grass vegetative stem			0.1 ± 0.07	1.1 ± 0.49	0.1 ± 0.10
grass flower stem			0.1 ± 0.47	4.1 ± 0.75	0.3 ± 0.18
grass seed/flowerhead			-	0.4 ± 0.25	0
Juncus		green	-	0.0 ± 0.03	0
		dead	-	0	0
Galium		green	0	-	0
		dead	0.0 ± 0.03	0	-
moss			0.1 ± 0.05	0	0.7 ± 0.06
			n = 8	n = 10	n = 10

0 = recorded in vegetation but not in diet. - = absent from vegetation and diet.
All results expressed as mean percentage ± s.e.m.

Table 6.7: Composition of the diets consumed by the red deer on the Calluna community.

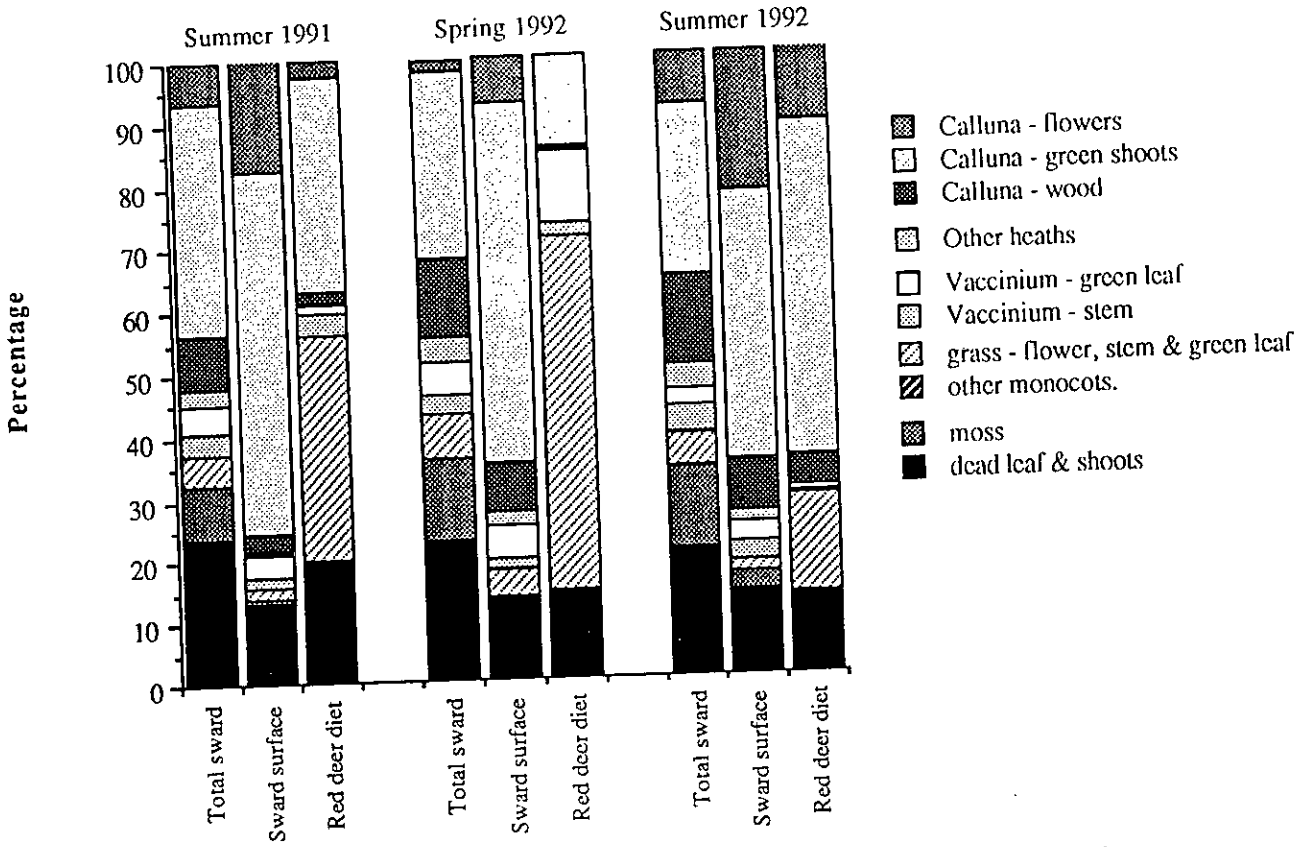


Figure 6.3: Composition of the diets consumed by the red deer on the Calluna community.

ovina, together accounted for approximately two-thirds of the material consumed by the red deer from the dwarf-shrub community. However, the levels of each varied between sessions. The proportion of the spring diet accounted for by green *Calluna vulgaris* shoots was significantly lower than recorded in either summer diet (Table 6.8). There was also a significant difference between the proportions of green *Calluna vulgaris* shoots in the summer 1991 and summer 1992 diets, with the higher proportion in 1992 being matched by higher proportions of dead shoots, wood and flowers.

The significant decrease from over 30 per cent to under 15 per cent in the amount of green *Calluna vulgaris* shoots in the spring 1992 diet relative to the summer 1991 diet was matched by a significant increase in green lamina of *Festuca ovina* resulting in this category making up 50 per cent of the diet. However, during the summer session in 1992 the proportions were reversed. Leaves of other grass species made little contribution to the diet of the red deer. Likewise, although there was a seasonal variation in the amount of grass flowerstem the overall contribution to the diet of this and the other grass morphological units remained relatively small.

The proportions of green and dead leaves of *Vaccinium myrtillus* in the diet were significantly higher during the spring experimental session. Additional species of dicotyledonous plants available were all but omitted along with grass-like monocotyledonous plants.

The Electivity Index values for the components in the diets consumed on the dwarf-shrub community are listed in Table 6.9. The changes in the amount of green *Calluna vulgaris* shoots in the diet of the red deer correspond to changes in selectivity from tolerance in summer 1991 to weak avoidance during the spring session and strong selection in summer 1992 relative to the proportion of this component recorded in the sward as a whole. Selectivity relative to availability at the sward surface showed a similar

Vegetation category			Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992	
Calluna	shoot	green	***	*	***	
		dead	ns	ns	*	
	wood		***	**	***	
	flower		**	***	***	
Erica	shoot	green	ns	ns	ns	
		dead	ns	ns	ns	
	wood		ns	ns	ns	
V. myrtillus	leaf	green	***	ns	***	
		dead	*	ns	**	
Vaccinium	stem	green	ns	**	ns	
		dead	ns	ns	ns	
Festuca	leaf	green	**	*	***	
		dead	**	***	ns	
Deschampsia	leaf	green	ns	ns	ns	
		dead	ns	ns	ns	
broad-leaved grass	leaf	green	ns	ns	ns	
		dead	ns	ns	ns	
grass vegetative stem			***	ns	***	
grass flower stem			ns	ns	ns	
grass seed/flowerhead			*	ns	*	$\phi\psi$
Juncus		green	ns	ns	ns	
Galium		dead	ns	ns	ns	
moss			ns	ns	ns	

ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$

ϕ = plot effect

ψ = plot x session interaction

Table 6.8: Summary of statistical analysis comparing the diets selected by the red deer from the Calluna community during each experimental session

Vegetation category			Summer 1991		Spring 1992		Summer 1992	
			Total	Surface	Total	Surface	Total	Surface
Calluna	shoot	green	0	-	-	- -	+ +	+
		dead	- -	- -	- -	- -	- -	-
	wood		- -	-	- -	- -	- -	-
	flower		-	- -	- -	- -	+	-
Erica	shoot	green	-	+ +	+ +	+ +	- -	- -
		dead	0	+ +			+ +	+ +
	wood		+ +	+ +			- -	
	flower		- -					
Empetrum			- -	- -	- -	- -	- -	- -
V. myrtillus	leaf	green	- -	-	+	+	-	-
		dead	+	+ +	+ +	+ +	+ +	+ +
	flower							
V. vitis-idaea	leaf	green	- -		- -	- -	- -	
		dead	- -				- -	
Vaccinium	stem	green	0	+	-	+	- -	- -
		dead	- -	-	-	-	- -	- -
Festuca	leaf	green	+ +	+ +	+ +	+ +	+ +	+ +
		dead	+ +	+ +	+ +	+ +	+ +	+ +
Deschampsia	leaf	green	- -	-	- -	- -	- -	- -
		dead	- -	- -	- -	- -	- -	- -
broad-leaf	leaf	green	+ +	+ +	+ +	+ +	+ +	+ +
		dead	+ +	+ +	+ +	+ +	+ +	+ +
vegetative stem			- -	+ +	+	+ +	- -	+ +
flower stem			+	-	+	+ +	+ +	+ +
seed/flowerhead				- -	+ +	+ +		
Juncus		green			- -	- -	- -	
		dead			- -		- -	
Galium		green	- -				- -	
		dead	- -	+ +	- -	- -		
moss			- -	- -	- -	- -	- -	- -

Abbreviations: + + = strong selection; + = weak selection; 0 = indifference; - = weak avoidance; - - = strong avoidance; blank = absent from vegetation and diet.
Total = relative to proportion in total sward. Surface = relative to proportion at sward surface.

Table 6.9: Selectivity indices for red deer diets from the Calluna community.

pattern of avoidance in the spring followed by selection in the summer. The other morphological units of *Calluna vulgaris* were avoided. In contrast, the response of the deer to *Erica* spp. was more variable.

Although green *Vaccinium myrtillus* leaves were only selected during the spring session, there was consistent selection for dead leaves of this plant species. Leaves of *Vaccinium vitis-idaea* were avoided along with dead *Vaccinium* stem.

Irrespective of season there was strong selection for lamina of *Festuca ovina* and broad-leaved grasses yet, strong avoidance of lamina of *Deschampsia flexuosa*. While consistent selection for the remaining morphological units of grass took place during the spring experimental session, the selection indices relative to the proportions of each category available in the sward as a whole or at the sward surface were variable for the summer diets.

6.3 DIET DIGESTIBILITY

6.3.1 *In vitro* digestibility.

The mean digestibility of the diets selected from each community by the oesophageal fistulated animals during each experimental session are listed in Table 6.10a and plotted in Figure 6.4a . Summaries of statistically significant differences are given in Table 6.10b and 6.10c.

The digestibility coefficients of the diets selected during each experimental period on the Lolium sward were similar. Likewise there were no differences between sessions in the digestibility of the diets selected from the Nardus grassland. In contrast, the diet chosen during the spring session on the Calluna community was significantly more digestible than that selected during either summer session.

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	0.802 ± 0.0041	0.796 ± 0.0089	0.818 ± 0.0161
Nardus	0.683 ± 0.0079	0.691 ± 0.0076	0.661 ± 0.0041
Calluna	0.485 ± 0.0116	0.714 ± 0.0289	0.487 ± 0.0015

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	ns	ns	ns
Nardus	ns	ns	ns
Calluna	***	ns	***

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	***	***	***
Spring 1992	***	**	ns
Summer 1992	***	***	***

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 6.10: *In vitro* digestibility of diets selected by red deer.

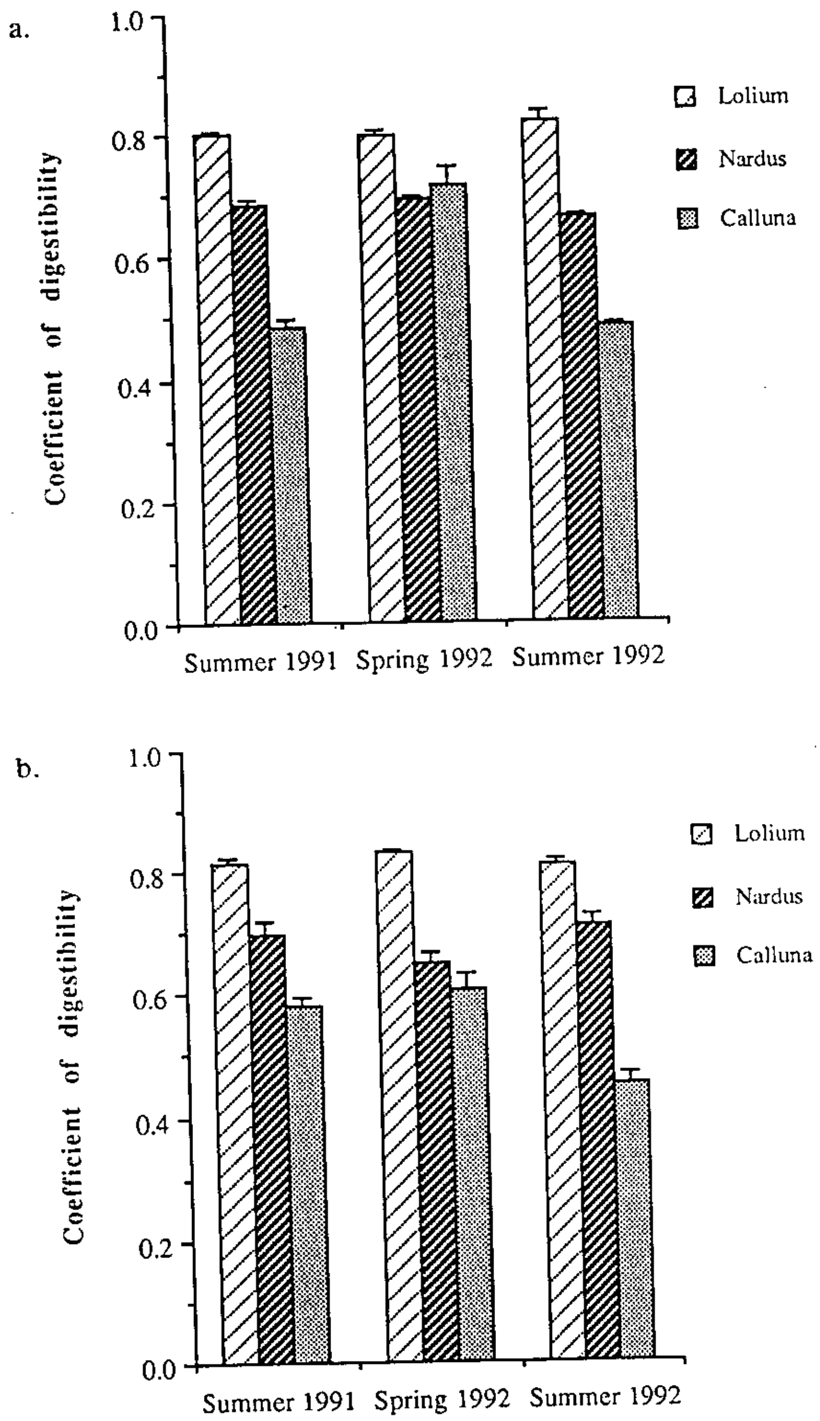


Figure 6.4: Effect of season and vegetation type on digestibility of diets selected by red deer as determined using: a. *in vitro* analysis; b. n-alkane analysis

During both summer sessions there were significant differences between the digestibility coefficients of the diet selected on each of the vegetation types with those of the diets consumed on the Lolium and Calluna swards highest and lowest respectively. However, in spring the digestibility of the diet selected on the Nardus grassland was similar to that of the diet consumed on the Calluna community.

6.3.2 Digestibility from n-alkanes

Equivalent results and statistical information for diet digestibility as determined using the n-alkanes technique have been plotted and tabulated in Figure 6.4b and Table 6.11a, 6.11b and 6.11c respectively.

Once again, the digestibility of the diet selected on the Lolium sward on each occasion was similar. While there were no differences between the diet selected on the Nardus grassland in summer 1991 and either of those consumed in 1992, the digestibility of the diet consumed in summer 1992 was significantly lower than that on the same sward in spring 1992. The coefficient of digestibility of the diet selected from the Calluna community in summer 1992 was significantly lower than that consumed in either of the previous sessions.

Once again during both summer sessions there were significant differences between the digestibility coefficients of the diets selected from each vegetation community, with that consumed on the Lolium sward highest and that on the Calluna community lowest. While the digestibility of the Calluna diet was also significantly lower than that on either grassland community in spring in contrast to the summer sessions there was no difference between the digestibilities of the diets chosen on the Lolium and Nardus swards.

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	0.813 ± 0.0089	0.833 ± 0.0035	0.810 ± 0.0063
Nardus	0.698 ± 0.0191	0.649 ± 0.0159	0.708 ± 0.0187
Calluna	0.578 ± 0.0134	0.604 ± 0.0267	0.450 ± 0.0187

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	ns	ns	ns
Nardus	ns	ns	*
Calluna	ns	***	***

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	**	***	**
Spring 1992	***	***	ns
Summer 1992	**	***	***

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 6.11: Digestibility of diets selected by red deer as determined using n-alkanes

6.4 INTAKE

6.4.1 Organic matter intake

Organic matter intakes (OMI) for the red deer on each community during each experimental session are listed in Table 6.12a and plotted in Figure 6.5a. Statistical differences are summarised in Table 6.12b and 6.12c.

The OMI by the red deer when grazing the Lolium pasture was lower in summer 1991 than in summer 1992. No differences between sessions were recorded in the amount consumed on either of the two indigenous communities.

During the experimental periods in summer 1991 and spring 1992 the OMI by the red deer was similar on each vegetation type. In contrast, there were significant differences between the amounts consumed on each community in summer 1992, with intake on the Lolium sward highest and that on the Calluna community lowest.

6.4.2 Digestible organic matter intake

The digestible organic matter intake (DOMI) values for the red deer on each community are listed in Table 6.13a and plotted in Figure 6.4b. Summaries of statistically significant differences are given in Table 6.13b and 6.13c.

The DOMI of the red deer on the sown sward in summer 1992 was significantly higher than that recorded during either of the two previous sessions. In contrast, DOMI on the indigenous grassland was similar during all three sessions. The DOMI recorded in spring 1992 on the Calluna community was significantly higher than that recorded during the summer session the same year.

In summer 1991 DOMI was significantly lower on the dwarf-shrub community than on either grassland community, During the spring session DOMI was higher on the sown

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	2.033 ± 0.2642	2.481 ± 0.2641	3.748 ± 0.1626
Nardus	2.437 ± 0.1040	2.158 ± 0.1108	2.398 ± 0.1217
Calluna	1.888 ± 0.1947	1.841 ± 0.2924	1.325 ± 0.0838

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	ns	**	ns
Nardus	ns	ns	ns
Calluna	ns	ns	ns

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	ns	ns	ns
Spring 1992	ns	ns	ns
Summer 1992	***	***	**

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 6.12: Organic matter intake of red deer (kg/day)

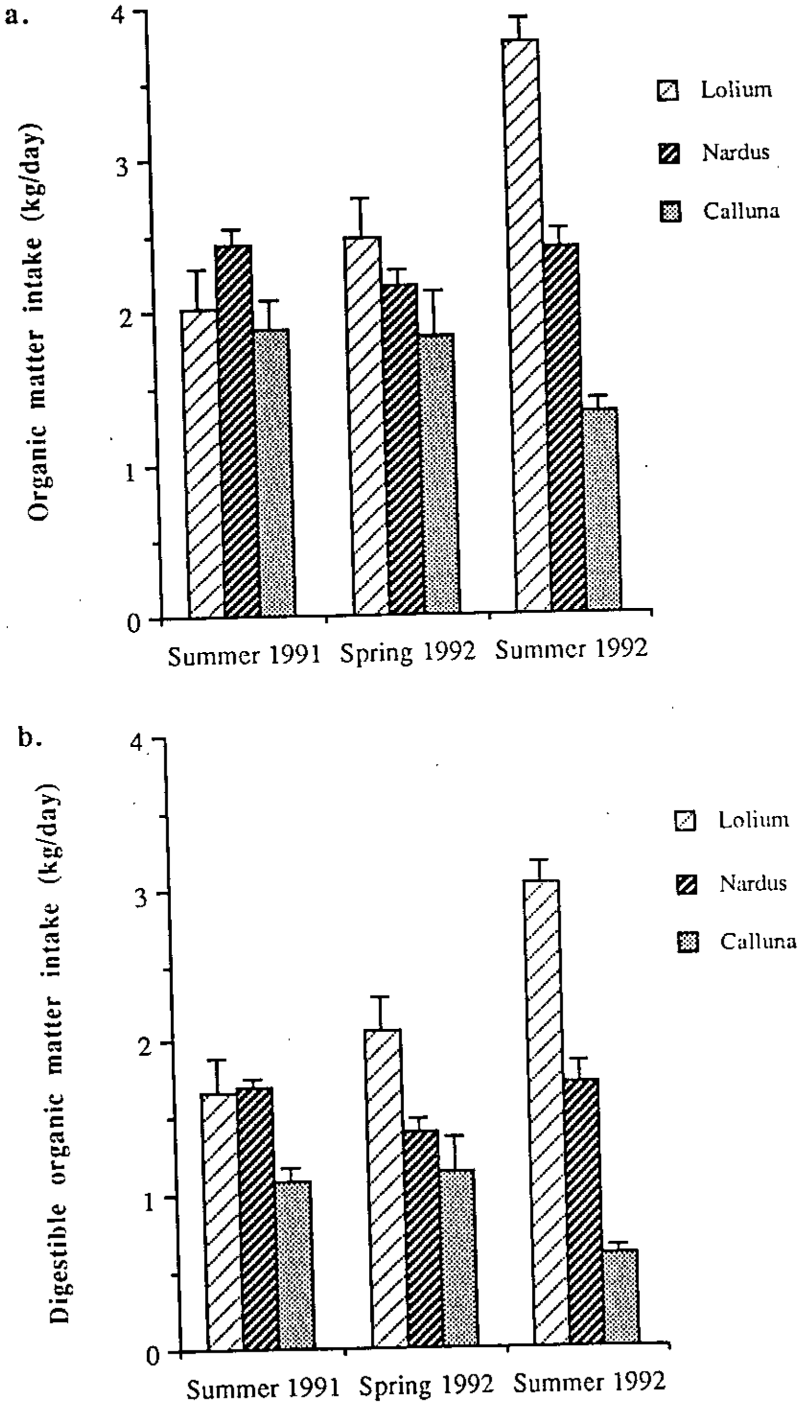


Figure 6.5: Effect of season and vegetation type on: a. organic matter intake; and b. digestible organic matter intake of red deer (kg/day).

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	1.659 ± 0.2256	2.068 ± 0.2231	3.034 ± 0.1295
Nardus	1.696 ± 0.0454	1.403 ± 0.0897	1.720 ± 0.1303
Calluna	1.085 ± 0.0917	1.135 ± 0.2276	0.600 ± 0.0560

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	ns	***	**
Nardus	ns	ns	ns
Calluna	ns	ns	*

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	ns	*	*
Spring 1992	*	**	ns
Summer 1992	***	***	***

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 6.13: Digestible organic matter intake of red deer (kg/day)

sward than on either indigenous community. DOMI on the sown sward was again highest in summer 1992, when a significant difference was also recorded between the DOMI on the Nardus and Calluna communities, with the latter lower.

6.5 GRAZING PATTERN

6.5.1 Total grazing time

The total grazing time of the red deer on each community during each experimental session are listed in Table 6.14a and plotted in Figure 6.6. Statistical differences are summarised in Table 6.14b and 6.14c.

The total grazing time on the Lolium sward during the summer 1991 session was significantly higher than that for the spring 1992 session. On the Nardus community the total grazing time of the red deer in summer 1992 was significantly lower than that recorded for either summer 1991 or spring 1992. The grazing time during the spring session on the Calluna community was significantly lower than that recorded for either summer session.

During the summer 1991 experimental session the total grazing time on the three vegetation types was similar. In contrast, during the spring 1992 session they were all significantly different with the grazing times recorded when the deer were selecting from the Nardus community and Lolium sward highest and lowest respectively. During summer 1992 the amount of time the deer spent grazing was significantly higher on the dwarf-shrub community than on either of the grassland communities.

6.5.2 Grazing pattern

The grazing pattern of the red deer on each vegetation type during each experimental session was also determined from the vibracorder data. The cumulative results for the measurement weeks in summer 1991 are depicted in Figure 6.7 as an example. The

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	599 ± 46.8	493 ± 15.5	518 ± 23.0
Nardus	621 ± 20.3	621 ± 24.3	500 ± 14.4
Calluna	672 ± 26.7	560 ± 20.4	679 ± 14.3

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	**	ns	ns
Nardus	ns	***	***
Calluna	**	ns	***

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	ns	ns	ns
Spring 1992	***	*	*
Summer 1992	ns	***	***

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communities

Table 6.14: Total grazing time of red deer (min/day).

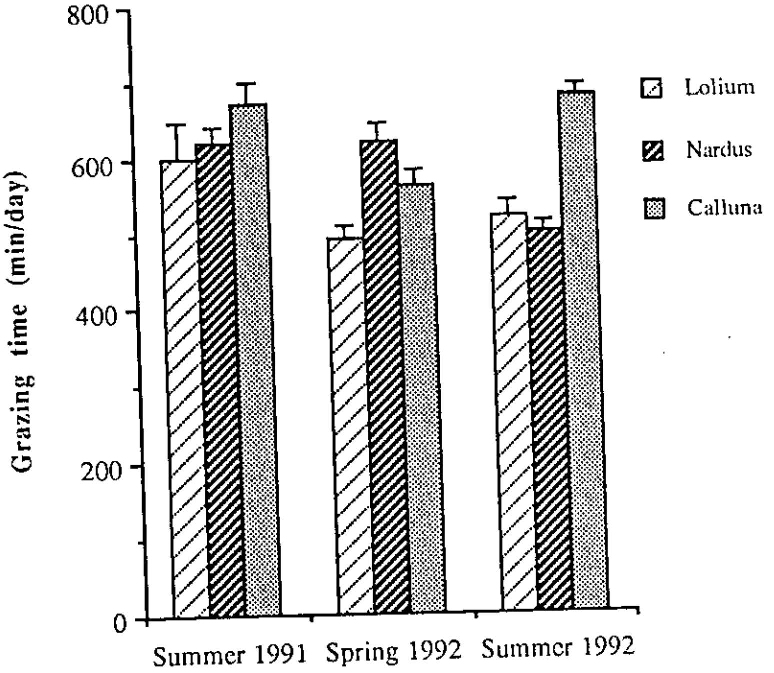


Figure 6.6: Effect of season and vegetation type on total grazing time of red deer.

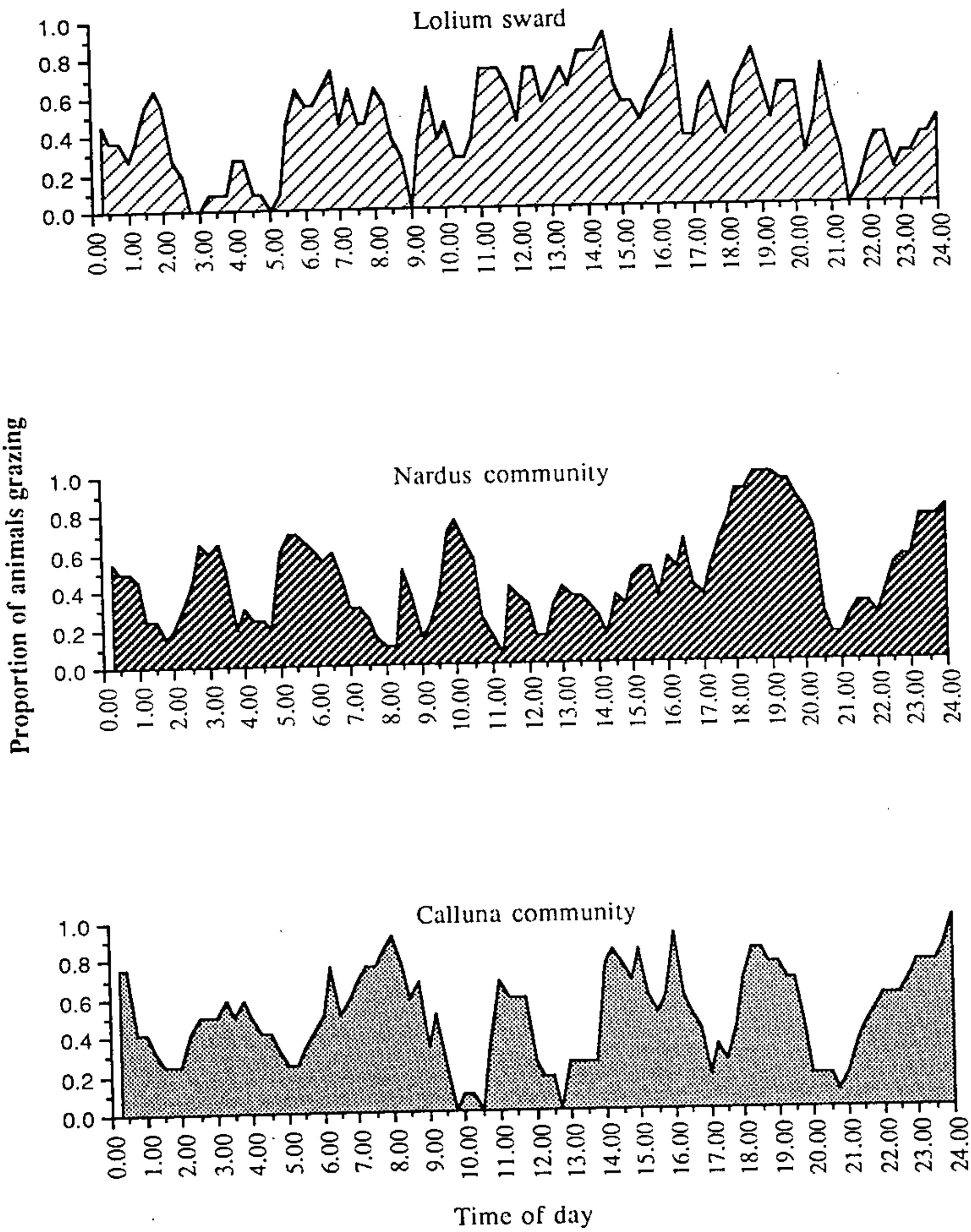


Figure 6.7: Effect of season and vegetation type on grazing pattern of red deer.

graphs plotted are similar to those generated by the two 1992 data sets. ,

As illustrated, within a given session the grazing pattern of the deer was similar irrespective of vegetation type, with the animals grazing during both day and night.

6.5.3 Synchronisation of grazing

Table 6.15 gives the kappa coefficient of synchronisation (K) of grazing, not grazing and overall activity on each vegetation type during each session, together with the variance and z statistics for each K. All but one kappa coefficient were significantly different from zero indicating that synchronisation was greater than would be expected by chance. The exception was the pattern of activity recorded on the Lolium sward in spring 1992.

In general the coefficient of synchronisation of not grazing for each session was slightly higher than that of grazing. There was no consistent order within sessions in the overall K calculated for each community. Consequently vegetation type did not influence the animals' synchronisation.

6.5.4 Bite rate

The mean and standard error of bite rates recorded for the red deer on each community during each experimental session are listed in Table 6.16a and plotted in Figure 6.8. Statistical differences are summarised in Table 6.16b and 6.16c.

The bite rate on the sown sward was higher in summer 1992 than it was during either of the previous two sessions. The only other significant difference between sessions was a lower bite rate on the Nardus community in summer 1992 in comparison with spring 1992.

		Grazing			Not grazing			Total		
Session	**Vegetation**	K	Var (K)	z	K	Var (K)	z	K	Var (K)	z
Summer 1991	Lolium	0.035	0.0003042	2.00	0.040	0.0006293	1.61	0.113	0.0002373	7.35
	Nardus	0.039	0.0000259	7.73	0.097	0.0018229	2.26	0.220	0.0013086	6.08
	Calluna	0.019	0.0002406	1.24	0.027	0.0011353	0.79	0.070	0.0005627	2.94
Spring 1992	Lolium	0.054	0.0001676	4.21	0.062	0.0003297	3.43	0.176	0.0000779	19.89
	Nardus	0.001	0.0002609	0.05	0.001	0.0024553	0.03	0.002	0.0002830	0.15
	Calluna	0.050	0.0000984	4.96	0.070	0.0005667	2.96	0.182	0.0002197	12.28
Summer 1992	Lolium	0.050	0.0003579	2.62	0.052	0.0004536	2.45	0.153	0.0001624	11.97
	Nardus	0.036	0.0001216	3.29	0.047	0.0004358	2.26	0.126	0.0001343	10.89
	Calluna	0.102	0.0003447	5.50	0.105	0.0003989	5.27	0.311	0.0001352	26.76

K = kappa coefficient of synchronisation
Var(K) = variance of K
z = z statistic for K

Table 6.15: Grazing synchronisation of red deer

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	35.7 ± 4.17	34.6 ± 1.99	45.0 ± 2.71
Nardus	44.7 ± 4.06	46.5 ± 3.44	34.4 ± 2.51
Calluna	38.4 ± 2.94	29.8 ± 1.85	37.8 ± 0.86

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	ns	*	*
Nardus	ns	ns	**
Calluna	ns	ns	ns

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	ns	ns	ns
Spring 1992	*	ns	**
Summer 1992	*	ns	ns

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites
ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$

Table 6.16: Bite rates of red deer (bites/min).

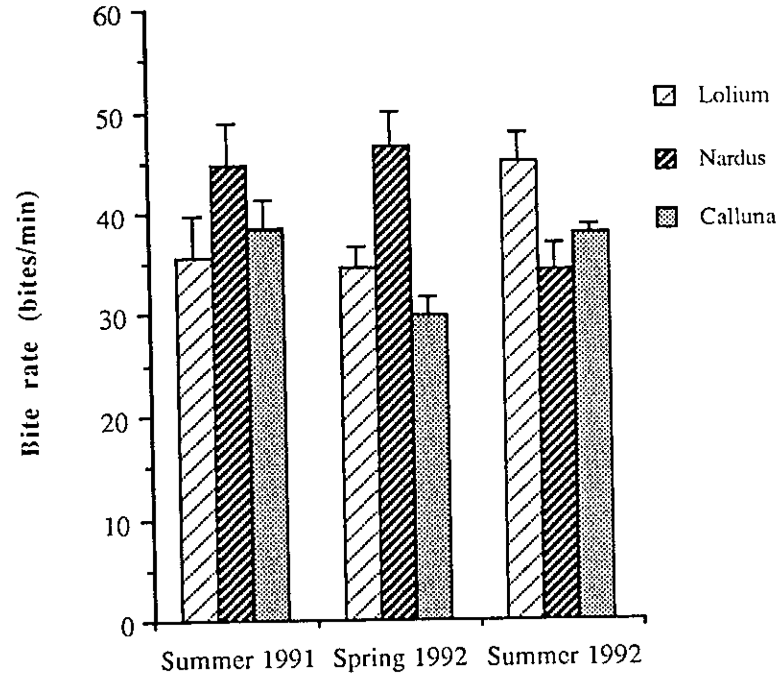


Figure 6.8: Effect of season and vegetation type on bite rate of red deer.

During summer 1991 the bite rates recorded on each of the three vegetation communities were similar. However in spring 1992 the bite rate for the red deer when grazing the Nardus community was higher than that on either the Lolium or Calluna communities. A significantly higher bite rate on the indigenous grassland in comparison with the sown sward was also recorded in summer 1992.

During summer 1991 no differences were recorded between the bite rates on each vegetation type. However, in spring 1992 the bite rate of the red deer was higher when grazing the Nardus community than on either the Lolium sward or Calluna community. In contrast, during the summer session later the same year the bite rate was higher on the Lolium sward than on the Nardus community.

6.6 DISCUSSION

Since the red deer studied had originated from farm stock, the animals were introduced to the intensive handling associated with a trial of this nature prior to the experimental work commencing. This period of habituation eliminated the stress-related behaviour initially exhibited when the animals were restrained (Diverio, Goddard and Gordon, 1993) and allowed the collection of data from calm animals.

During all three experimental sessions persistent difficulties were encountered capturing the red deer. Although inconvenient, this did not appear to distress the animals or altered their subsequent behaviour. In the case of the oesophageal fistulated animals, however, the ensuing activity frequently led to partial or complete sample loss. While this is unlikely to have affected results of the subsequent microscopic examinations to determine diet composition, the recurring loss of the liquid fraction of the extrusa samples may have influenced the *in vitro* digestibility determinations. Cell contents will have been released into the salivary fraction during mastication and failure to include this fraction in the subsequent *in vitro* digestibility analysis would be expected to lead to an underestimation of the coefficient of digestibility of the diet originally selected (Langlands, 1966). However, during the microscopic examinations it was noted that, even when sample collection had been complete, the red deer extrusa samples consisted of fragments of plant material which were larger and less damaged than those found in the samples from either the goats or guanacos. This implies the red deer chewed prehended material less prior to swallowing. This will have resulted in only relatively small quantities of cell contents being released into the saliva, and may account for the *in vitro* digestibility values of the extrusa samples being similar to those estimated using n-alkanes.

The red deer were more selective when grazing on the two heterogeneous communities than when on the relatively homogeneous established sown sward. Although there was selection and avoidance of green and dead leaf respectively on the Lolium sward the proportions of broad-leaved grasses, *Trifolium repens* and other dicotyledonous plants in the diet were similar to those present in the sward. In other studies diets of red deer on similar vegetation have been reported to contain higher and lower proportions of ryegrass and white clover respectively relative to proportions in the sward (Ataja *et al.*, 1992). Ataja *et al.* (1992) suggest the lower content of clover in the diet may be due to its lower height in the grazing canopy. This agrees with the selectivity indices calculated during the current study which indicated that the red deer were consuming sward components in similar proportions to those present near the sward surface.

On the Nardus community the deer confined their grazing to the species rich inter-tussock areas, resulting in broad-leaved species of grass again being the main dietary component. This agrees with observations made under free-ranging conditions when deer were recorded as closely cropping Agrostis/Festuca grassland, while areas dominated by *Nardus stricta* were less heavily grazed (Watson and Staines, 1978).

While red deer have a digestive system adapted for a diet containing both graminoids and browse (Hofmann, 1985), they are primarily adapted to make use of the cell-wall content of plant material they consume and consequently would be expected to graze to a greater degree than they browse. Certainly, grasses made a substantial contribution to the diet on the dwarf-shrub community despite graminoid species accounting for only a small proportion of the point quadrat hits (Chapter Four). The proportion of grasses consumed was inversely proportional to the consumption of green *Calluna vulgaris* shoots, with together these two vegetation categories dominating the diets selected. As there was consistent selection for grass irrespective of season or session, while in contrast green shoots of *Calluna vulgaris* were only selected in summer 1992 it would appear that the overall contribution of each category was dictated by the availability of the former. This pattern is consistent with the observation of Milne and Grant (1978) that the proportion of *Calluna vulgaris* in diets of sheep was inversely related to the quantity of available grass. It also concurs with previous studies of free-ranging red deer which found the proportions of heather higher in winter and spring (Jensen, 1968; Hobson *et al.*, 1976; Yalden, 1978) when grass quality and quantity are generally lower, although Welch (1984a) found dung volumes on sites featuring different graminoid species were similar where *Calluna vulgaris* had roughly equal cover and height, suggesting grazing of subsidiary grasses or *Juncus* spp. was determined by usage of *Calluna vulgaris*.

Few of the minor components encountered during the vegetation surveys of the indigenous communities were selected by the red deer. Similarly, there was no evidence of a seasonal change in diet selection in response to the seasonal changes in the proportions or digestibility characteristics of individual vegetation categories within any of the three swards. Contributing to this consistency are the selectivity restrictions imposed on the deer by their comparatively broad, flat mouths which will reduce their ability to discriminate between particular plant species and/or plant parts (Gordon and Illius, 1988). Consequently under free-ranging conditions seasonal changes in diet selection occur at the community level (Charles, McGowan and East, 1977; Gordon, 1989c).

The consistency of the diets selected from each vegetation type across seasons and year indicates that although red deer are considered to be mixed feeders consuming a variable diet, this plasticity will have been a response to changes in the specific opportunities available. When the composition of the vegetation on offer is constant, so too is diet composition.

It is difficult to explain the organic matter intake on the Lolium sward recorded in summer 1992 being significantly higher than that during the previous summer. The consistency of the results obtained from each animal as reflected in the standard error of the mean intake value rules out undetected pellet loss by one of the animals lowering the C_{32}-alkane concentration in the faeces.

With the exception of this estimate for consumption on the sown sward during the second summer the organic matter intake of the deer remained constant irrespective of vegetation type or season. As the red deer used during this study were castrates they did not experience the direct testosterone-induced cessation of food intake associated with rutting stags but still followed the seasonal rhythm of food intake exhibited by both sexes in response to changes in daylength. As a result, peak food intake for these animals would be expected in late spring-early summer and the lowest intake during mid-winter (Suttie *et al.*, 1983). Seasonal differences in voluntary food intake during the current study were therefore unlikely.

When differences in liveweight are taken into account the intake values on the indigenous grassland and dwarf-shrub community are similar to those for castrates fed *Agrostis-Festuca* spp. and heather in spring (Milne *et al.*, 1978). Likewise, if the inexplicable intake for summer 1992 on the Lolium sward is excluded the intake values determined are similar to those estimated for weaner red deer stags (Semiadi *et al.*, 1993a) and mature hinds (Heydon *et al.*, 1993) grazing perennial ryegrass/white clover pastures. The latter trial used the n-alkane technique to measure intake and diet digestibility, and generated similar digestibility values for summer sessions on plots with similar high availabilities of herbage to those recorded during the current study. Values for diet digestibility on the Lolium sward as determined from *in vitro* analysis on extrusa samples in this study are slightly lower than those for extrusa samples collected by weaner (Ataja *et al.*, 1992) and mature (Semiadi *et al.*, 1993a) castrates grazing a conventional perennial ryegrass/white clover sward in New Zealand. No equivalent data for diet digestibility of free-roaming red deer on indigenous communities is available for comparison.

No difference was found in the total grazing time on the Lolium sward in summer 1992 compared with summer 1991 to relate to the differences in intake observed. Instead neither the difference in grazing time identified on this sward nor those found between sessions on the indigenous communities can be linked to changes in intake. Likewise the pattern of differences in grazing times on different communities within a given experimental session do not correspond to differences in digestible organic matter intake.

In comparison with recorded values for stags on indigenous pasture during summer (Clutton-Brock, Guiness and Albon, 1982), the total grazing times recorded during the current study on the indigenous communities are generally comparable, but with those on the Lolium sward consistently lower. The values from the Lolium pasture are also slightly lower than those of stags and hinds on a grass/clover sward in New Zealand (Semiadi *et al.*, 1993b). However, the daily patterns of grazing are similar. Likewise the activity profiles created from the vibracorder data during the current study agree with the conclusions of Mitchell, Stains and Welch (1977) that red deer are diurnal with peaks of activity at dawn and dusk. The rates of biting observed during the current study were substantially lower than those previously reported for red deer grazing a grass/clover sward (Semiadi *et al.*, 1993b). However, Semiadi *et al.* (1993) recorded time to take twenty bites and rates of biting estimated using the 20-bite method have been shown to be substantially greater than those measured using the 100-bite method (Illius, 1989). In general rate of biting did not vary with sward type which agrees with observations made on wild red deer (Clutton-Brock, Guiness and Albon, 1982).

6.7 SUMMARY

1. The diets consumed by the red deer on each vegetation community were notably consistent across seasons and years.

2. On the Lolium sward the red deer selected green leaf of all plant groups found at or near the sward surface.

3. When grazing on the Nardus community the deer demonstrated more discrimination between plant genera and species than on the Lolium sward. The dominant tussock grass was consistently avoided, and instead the deer confined their grazing to the inter-tussock areas. As a result green leaves of broad-leaved grasses was the main dietary component.

4. When the deer grazed the dwarf-shrub community *Calluna vulgaris* was generally avoided, with its contribution to the diet inversely proportional to the consumption of graminoid species.

5. While diet digestibility was dictated by vegetation type, OMI was relatively consistent. Thus diet digestibility varied more than intake, and this is reflected in the DOMI results.

6. The red deer grazed during both day and night. Neither vegetation type nor season influenced total grazing time or bite rate of the deer.

CHAPTER SEVEN

DIET COMPOSITION AND INGESTIVE BEHAVIOUR OF SOUTH AMERICAN CAMELIDS

7.1 REVIEW

The guanaco (*Lama guanicoe*) and vicuna (*Lama vicugna*) are indigenous hoofstock of the South American high plains and, together with the domesticated llama (*Lama glama*) and alpaca (*Lama pacos*) belong to the family Camelidae, which also includes the dromedary and bactrian camels. Camelids appear in the late Eocene fossil record and were one of the first of the modern families of Artiodactyls (Franklin, 1982). They are separated from the Infraorder Pecora into the suborder Tylopoda (pad-footed) because they differ in stomach morphology (three compartments), absence of horns or antlers and the replacement of hooves with callous pads ending in claws (Novoa and Wheeler, 1982). Inconsistencies and confusion on lamoid classification are found throughout the literature as illustrated by Franklin (1982) and Novoa and Wheeler (1982). Most European classifications place all four species in the same genus, *Lama*, whereas those of North and South America use two genera, recognising the vicuna as a separate genus *Vicugna*.

Of the four species of South American camelid the guanaco has the broadest geographical and altitudinal distribution, with the latter ranging from sea level to 4250 metres (Franklin, 1982) and four geographical subspecies have been described (Novoa and Wheeler, 1982). In contrast, the llama and alpaca populations are essentially restricted to the Bolivian and Peruvian altiplano of the Andes Mountains, an extensive high plateau zone between 3600 and 3800 meters above sea level. Vicuna distribution is also limited to this area but may include altitudes of up to 4800 metres above sea level.

There are two general climatological seasons in the part of the Andes most densely populated by camelids; a mildly warm, rainy growing period from December to April and a cold dry period from May to November. Precipitation is erratic and limited, with approximately 80 per cent of the rainfall occurring during the wet season and the remainder during the dry season in the form of hail and snow (Sumar, 1988).

Rangeland plant production follows this pattern with an abundance of forage in the wet season and scarcity in the dry season. Bunchgrasses of the genera *Stipa*, *Festuca* and *Calamagrostis* are the dominant vegetation (Bryant and Farfan, 1984). As with other high altitude animals, camelids are adapted to survive extreme conditions such as low ambient oxygen, dehydration and radical temperature fluctuation (Mario and Morrison, 1963).

Camelids share a number of common behavioural characteristics, some differing from most other livestock. For example, they defecate and urinate in relatively confined areas (latrines) (Sumar, 1988). For guanaco and vicuna this has the short-term primary function of marking territories. In the long-term it has a fertilising effect, particularly after rain, and possibly reduces the risk of infestation by internal parasites.

The differences in morphology, histology and motility of the forestomach mentioned can be accounted for by independent development following separation of the Tylopoda and Pecora suborders from primordial species which were simple stomached (Engelhardt and Heller, 1985). Like true ruminants camelids have a digestive system which includes a forestomach with a population of bacteria and protozoa which breaks down cellulose into short-chained fatty acids and have evolved the same general characteristics of regurgitation and remastication of food. However, their forestomach is anatomically different, having only three compartments (referred to as C1, C2 and C3). Studies of camelid gross anatomy, microscopic anatomy and physiology indicate that C1 and C2, which account for eighty-three and six per cent of stomach volume respectively (Vallenas, Cummings and Munnell, 1971), are comparable to some extent with the rumen and reticulum in conventional ruminants. The third compartment (C3) accounts for eleven per cent of the stomach volume (Vallenas, Cummings and Munnell, 1971) and has been considered the homologue of the true ruminant abomasum (Johnson, 1983). Elsewhere the proximal four-fifths of this tubular organ has been viewed as an omasal homologue and the distal one-fifth, which corresponds to the site of gastric glands, as an abomasal homologue or hindstomach (Heller, Gregory and Engelhardt, 1984).

The basic pattern of motility of these stomach compartments has been shown to differ markedly in sequence and number of contractions in comparison with ruminants (Heller, Gregory and Engelhardt, 1984) although regulation of forestomach motility is similar (Engelhardt and Heller, 1985). The particular sequence of contraction which have evolved in camelids results in an effective microbial digestion of the rather dry forestomach contents by allowing maximum mixing of food with bicarbonate buffer and with the micro-organisms of the forestomach without increasing the rate of forestomach emptying (Heller, Gregory and Engelhardt, 1984). In addition it facilitates a long, variable retention time of particles and the absorption of water and solutes (Engelhardt and Heller, 1985).

Retention time of feed particles in the fermentation chamber of the forestomach is significant as it largely governs the amount of fibre digested, and camelids have adapted to conditions where forage quality may be limited by reducing intake and selectivity increasing transit time of the digesta through the digestive tract to better accommodate microbial attack of the highly structured carbohydrate diet. Thus, although large particulate transit time is increased, with llamas retaining particles for a comparatively longer period of time as compared to cattle or sheep, the passage of liquid and smaller particles is more rapid (Clemens and Stevens, 1980; Engelhardt, Rubsamen and Heller, 1984). This high fluid flow rate supports a more rapid microbial fermentation through a higher buffering capacity and improves outflow of the soluble products of microbial fermentation. In addition, histochemical and biochemical analysis as well as absorption studies have revealed that the function of the glandular epithelium in the llama forestomach is different from that of ruminal epithelium (Rubsamen and Engelhardt, 1979) and adapted for greater digestive efficiency (Vallenas, Cummings and Munnell, 1971). Consequently, absorption rates for the llama forestomach have been recorded as two to three times those of sheep and goat rumens (Rubsamen and Engelhardt, 1979). Such features have been suggested as contributing to the greater digestion coefficients which have been reported for llama than sheep on low and medium quality diets (Hintz, Schryver and Halbert, 1973), although digestion coefficients were similar on high quality diets (Bryant, 1987, cited in San Martin and Bryant, 1989).

Most information on voluntary intake in camelids comes from comparative studies with sheep under penned conditions. Reviewing previous studies San Martin and Bryant (1989) concluded that the voluntary intake for llama was lower than that of sheep on a metabolic weight basis. They also concluded that, with some exceptions, consumption in the dry season was similar to or greater than in the rainy season. A higher intake in the dry season when dietary quality is lower is postulated as resulting from either an increase in gut capacity in response to lower diet quality during the dry season, or the high water content of plants during the rainy season.

The dental anatomy of camelids also sets them apart from ruminants. The single upper incisor of both old and new world camelids has migrated caudally and evolved to a caniniform shape and function (Esteban and Thompson, 1988) while the six lower incisors make contact with a toothless dental pad. These incisors are firmly fixed in the mandible, similar to the dentition of sheep and goats but in contrast to the loose attachment of bovine teeth (Fowler, 1989). In the case of vicunas these sharp lower incisors differ in shape and structure from those of other artiodactylids being more like the continuously erupting incisors of rodents (Miller, 1924).

The upper lip of the camelid is split by a labial cleft and can be considered prehensile (Wilson, 1989). As a result of the split each side of the lip can be manipulated independently to investigate a potential food item and draw it to the teeth. The vertical and horizontal mandible movement allows for efficient use of the premolars and molars in cutting and grinding of fibrous feeds.

In the Peruvian Altiplano llama and alpaca are mixed with sheep and managed together (San Martin and Bryant, 1989). However, few studies have compared dietary composition between these herbivores to understand how they partition the forage resource, although it has been observed that, while alpaca used more moist bottomlands, llama preferred to graze drier areas dominated by tall and coarse bunchgrasses (Franklin, 1982).

Such studies would have to take into account seasonal differences in diet composition. Using microhistological analyses of faecal material Bryant and Farfan (1984) established grass consumption by alpaca was highest during the driest months and declined during the early wet season when forbs increased. Similarly, consumption of grass-like monocotyledonous plant species was inversely related to grass in the diet. Reiner and Bryant (1986) also found that where grass was available it comprised the bulk of the alpaca diet, but on a site with low grass availability and abundant sedges diets were dominated by sedges.

In general the guanaco is acknowledged as being a generalist herbivore, consuming a diet consisting of a broad range of forage types (Raedeke, 1980). This may be the result of the evolution of the guanaco without any major herbivore competitors or alternatively that it is in part a response to the recent increase in competition with domestic sheep. Certainly the consumption of particular forage species has been linked to availability, and a shift in diet composition during periods of competition with sheep has been suggested (Raedeke, 1980).

RESULTS

7.2 DIET COMPOSITION

7.2.1 The Lolium sward

The mean proportions of components in the diet selected by the guanacos from the sown sward on each occasion are tabulated and depicted in Table 7.1 and Figure 7.1 respectively.

The diet selected by the camelids from the Lolium sward was composed almost entirely of graminoid species, with dicotyledonous plants only accounting for between 1-6 per cent of the material consumed. Green lamina of broad-leaved grasses was the main dietary component on all three occasions. The significant decrease (Table 7.2) in the proportion of the diet accounted for by this category from over 90 per cent in summer 1991 to 70 per cent in 1992 corresponds to a significant increase in the amount of dead lamina in the diets in 1992. The only indication of seasonal variation in diet composition was a significantly higher amount of seed/flowerhead in the diets selected during the spring session.

The Electivity Index values for the components identified in the camelid diets are listed in Table 7.3. In general there was selection for green lamina, flowerstem and seed/flowerhead of the graminoid species. Dead lamina and vegetative stem were avoided relative to the proportions of these components in the sward as a whole but selected relative to the composition of the sward surface. Although green leaves of *Trifolium repens* were consistently avoided, during 1992 there was tolerance or selection of clover petiole.

7.2.2 The Nardus community

The mean proportions of components in the diet consumed on the Nardus community during each experimental session are tabulated and depicted in Table 7.4 and Figure 7.2

Vegetation category			Summer 1991	Spring 1992	Summer 1992
broad-leaved grasses	leaf	green	91.3 ± 2.21	71.2 ± 2.06	72.5 ± 3.70
		dead	2.9 ± 0.60	5.9 ± 1.02	13.6 ± 2.43
grass vegetative stem			0.7 ± 0.38	5.9 ± 1.21	4.4 ± 0.81
grass flowerstem			2.5 ± 1.61	5.1 ± 0.81	3.3 ± 1.18
grass seed/flowerhead			1.3 ± 0.72	8.9 ± 2.19	0.2 ± 0.10
Trifolium repens	leaf	green	1.2 ± 0.18	1.1 ± 0.57	2.8 ± 1.18
		dead	0	0.0 ± 0.01	0.1 ± 0.01
	petiole		0	0.2 ± 0.21	1.2 ± 0.63
	flower		-	-	0
other dicots	leaf	green	0	± 1.04	1.2 ± 0.86
		dead	0	0	0.0 ± 0.05
	stem		0	0	0
	flower		-	0.1 ± 0.08	0.3 ± 0.20
moss			-	-	0.2 ± 0.17
			n = 3	n = 11	n = 7

0 = recorded in vegetation but not in diet. - = absent from vegetation and diet.

All results expressed as mean percentage ± s.e.m.

Table 7.1: Composition of the diets consumed by the guanacos on the Lolium community.

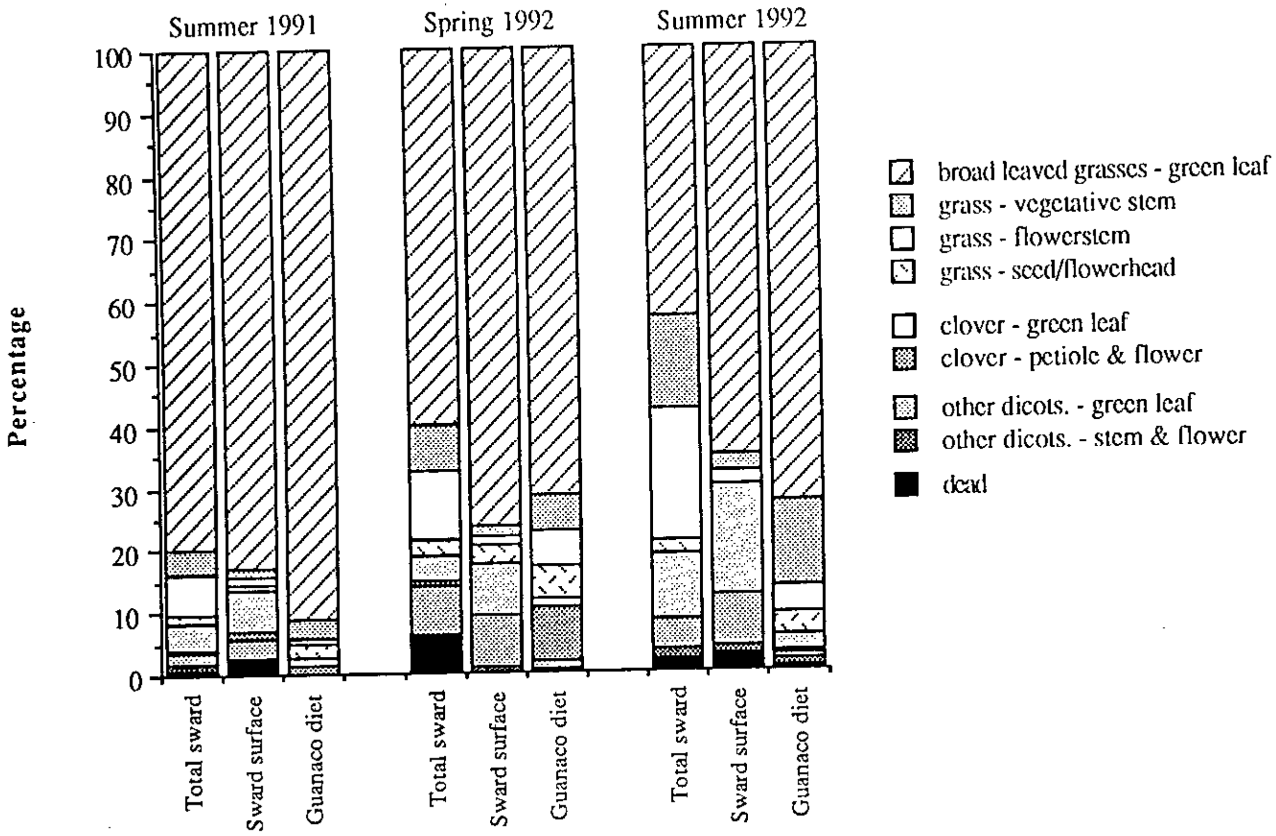


Figure 7.1: Composition of the diets consumed by the guanacos on the Lolium sward.

Vegetation category			Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
broad-leaved grasses	leaf	green	**	**	ns
		dead	ns	*	*
grass vegetative stem			*	ns	ns
grass flowerstem			ns	ns	ns
grass seed/flowerhead			***	ns	***
Trifolium repens	leaf	green	ns	ns	ns
		dead	ns	ns	ns
	petiole		ns	ns	ns
other dicots	leaf	green	ns	ns	ns
		dead	ns	ns	ns
	flower		ns	ns	ns
moss			ns	ns	ns

ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$
ϕ = plot effect
ψ = plot x session interaction

Table 7.2: Summary of statistical analysis comparing the diets selected by the guanacos from the Lolium sward during each experimental session

			Summer 1991		Spring 1992		Summer 1992	
Vegetation category			Total	Surface	Total	Surface	Total	Surface
broad-leaved grasses	leaf	green	+	+	+	-	+ +	+
		dead	-	0	-	+ +	0	+ +
grass vegetative stem			- -	-	-	+ +	- -	+
grass flowerstem			+	+	+	+ +	+	+
grass seed/flowerhead			+ +	+	+ +	+ +	+ +	+ +
Trifolium repens	leaf	green	- -	- -	- -	- -	- -	- -
		dead	- -		- -		- -	+ +
	petiole		- -	- -	+	+ +	0	+ +
	flower						- -	
other dicots	leaf	green	- -	- -	- -	- -	- -	- -
		dead	- -		- -		- -	+ +
	stem		- -	- -	- -	- -	- -	- -
	flower				+	- -	+ +	+ +
moss							+ +	+ +

Abbreviations: + + = strong selection; + = weak selection; 0 = indifference; - = weak avoidance; - - = strong avoidance; blank = absent from vegetation and diet.
Total = relative to proportion in total sward. Surface = relative to proportion at sward surface.

Table 7.3: Selectivity indices for guanaco diets from the Lolium sward.

Vegetation category			**Summer 1991**	**Spring 1992**	**Summer 1992**
Nardus	leaf	green	0.4 ± 0.22	1.6 ± 0.66	0.8 ± 0.24
		dead	0.3 ± 0.33	0.2 ± 0.13	0.1 ± 0.07
broad-leaved grasses	leaf	green	57.9 ± 14.87	52.8 ± 4.82	47.4 ± 5.06
		dead	13.1 ± 5.39	15.9 ± 4.42	13.2 ± 1.70
Festuca	leaf	green	2.9 ± 2.21	1.5 ± 0.76	0.2 ± 0.22
		dead	0.3 ± 0.25	0.5 ± 0.17	0.2 ± 0.14
Deschampsia	leaf	green	3.0 ± 1.38	9.9 ± 2.40	2.9 ± 1.00
		dead	0.2 ± 0.17	1.3 ± 0.56	0.5 ± 0.18
grass vegetative stem			6.6 ± 0.08	4.4 ± 0.54	3.2 ± 0.07
grass flowerstem			1.8 ± 1.31	5.3 ± 1.00	8.9 ± 0.72
grass seed/flowerhead			6.5 ± 0.78	2.5 ± 1.84	22.4 ± 1.76
Carex	all	green	0	0	0
		dead	-	0	0
Luzula	flower		-	2.6 ± 2.35	-
	leaf	green	0	0	0
		dead	0	0	0.0 ± 0.05
other monocots.	all	green	0	-	0
		dead	0	-	0
Galium	all	green	3.1 ± 2.72	0	0.1 ± 0.08
		dead	0.2 ± 0.17	-	0
Vaccinium	all	green	0	0	0
		dead	0	0.5 ± 0.52	0
Potentilla	all	green	2.8 ± 2.02	0	0
		dead	0.8 ± 0.83	0	-
other dicots.	all	green	0	-	-
moss			0.2 ± 2.41	0.9 ± 2.36	0.1 ± 5.35
			n = 3	n = 5	n = 14

0 = recorded in vegetation but not in diet. - = absent from vegetation and diet.

All results expressed as mean percentage ± s.e.m.

Table 7.4: Composition of the diets consumed by the guanacos on the Nardus community.

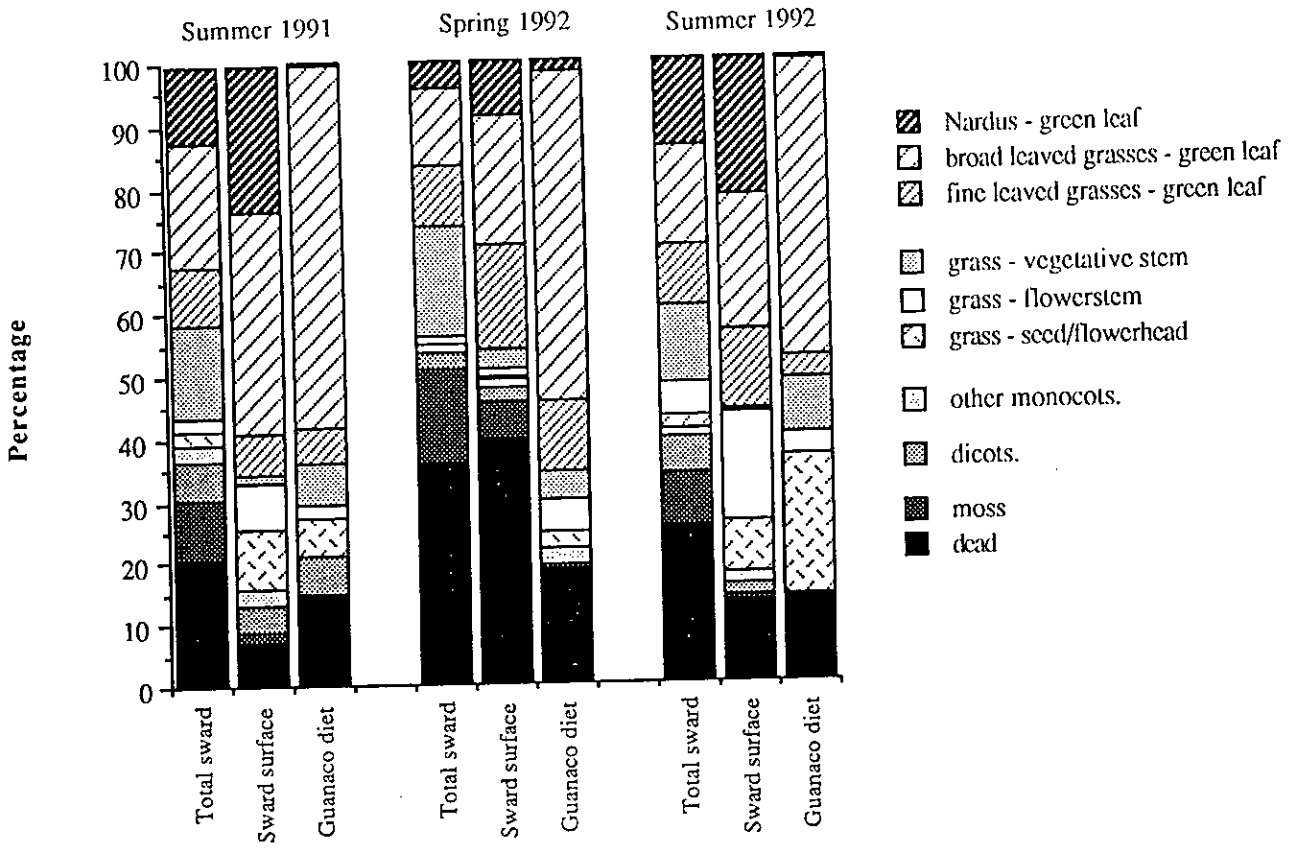


Figure 7.2: Composition of the diets consumed on the Nardus community by the guanacos.

respectively.

The dominant species of grass never accounted for more than 2 per cent of the diet selected by the guanacos. Instead the camelids confined their grazing to the inter-tussock area, and in particular the broad-leaved species of grass found there. Green lamina of these species accounted for approximately 50 per cent of the diet. Dead lamina of the same grasses also made a consistent contribution of over 13 per cent of the material selected. Green lamina of the species of fine-leaved grasses found in the inter-tussock areas made contributions of up to 10 per cent, yet the amount of dead lamina of these species consumed was small. There was a dramatic increase (Table 7.5) in the amount of seed/flowerhead in the diet in summer 1992 resulting in this category accounting for over a fifth of the material consumed.

Apart from flowers of *Luzula* spp in the spring diet grass-like monocotyledonous plants were practically omitted from the diet. Similarly, if more emphasis is given to the 1992 results, because of the fact only one oesphageal fistulated animal was available in 1991, then the amount of dicotyledonous plants recorded was also negligible.

The associated Electivity Index values for components identified in the diets consumed on each occasion are listed in Table 7.6. Both green and dead lamina of *Nardus* were consistently strongly avoided. Likewise lamina of *Festuca ovina* was avoided. In contrast there was generally strong selection for both green and dead lamina of broad-leaved species of grass. On balance *Deschampsia flexuosa* was also selected but the response of the guanacos to this species of grass was more variable. In comparison with the proportion in the sward as a whole vegetative stem was avoided; but when the amount in the diet was compared with the availability of this component at the sward surface selection occurred. The only indication of a seasonal change in selectivity was a switch to strong selection for flowerstem during the spring experimental session. However,

Vegetation category			**Summer 1991 v. Spring 1992**	**Summer 1991 v. Summer 1992**	**Spring 1992 v. Summer 1992**	
Nardus	leaf	green	ns	ns	ns	ϕ
		dead	ns	ns	ns	
broad-leaved	leaf	green	ns	ns	ns	
grasses		dead	ns	ns	ns	ϕ
Festuca	leaf	green	ns	**	*	ψ
		dead	ns	ns	ns	ϕ
Deschampsia	leaf	green	*	ns	**	
		dead	ns	ns	ns	
grass vegetative stem			ns	ns	ns	
grass flowerstem			ns	*	ns	
grass seed/flowerhead			ns	**	***	
Luzula	flower		ns	ns	*	
		dead	ns	ns	ns	
other monocots.	all	green	ns	ns	ns	
		dead	ns	ns	ns	
Galium	all	green	***	***	ns	ϕ
		dead	ns	ns	ns	
		dead	***	ns	***	ϕψ
Potentilla	all	green	ns	ns	ns	
		dead	ns	ns	ns	
moss			ns	ns	*	

ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$
ϕ = plot effect
ψ = plot x session interaction

Table 7.5: Summary of statistical analysis comparing the diets selected by the guanacos from the Nardus community during each experimental sessio

Vegetation category			Summer 1991		Spring 1992		Summer 1992	
			Total	Surface	Total	Surface	Total	Surface
Nardus	leaf	green	- -	- -	- -	- -	- -	- -
		dead	- -	- -	- -	- -	- -	- -
broad-leaved grasses	leaf	green	+ +	+	+ +	+ +	+ +	+ +
		dead	+ +	+ +	+ +	+ +	+ +	+ +
Festuca	leaf	green	-	-	- -	- -	- -	- -
		dead	- -	+ +	- -	- -	- -	- -
Deschampsia	leaf	green	-	+	+ +	+	+	0
		dead	- -	-	+	+	+	+ +
grass vegetative stem			-	+ +	- -	+	- -	+ +
grass flowerstem			-	- -	+ +	+ +	+	-
grass seed/flowerhead			+	-	+ +	+ +	+ +	+ +
Carex	all	green	- -		- -	- -	- -	- -
		dead			- -	- -		
Luzula	flower				+ +	+ +		
	leaf	green	- -	- -	- -	- -	- -	- -
		dead	- -		- -	- -	- -	- -
other monocots.	all	green	- -				- -	
		dead	- -				- -	
Galium	all	grean	-	+	- -	- -	- -	- -
		dead	-	-			- -	
Vaccinium	all	green	- -	- -	- -		- -	
		dead	- -		+ +	+ +	- -	
Potentilla	all	green	+	+	- -	- -	- -	- -
		dead	+ +	+ +	- -	- -		
other dicots.	all	green	- -	- -				
moss			- -	- -	- -	- -	- -	- -

Abbreviations: + + = strong selection; + = weak selection; 0 = indifference; - = weak avoidance; - - = strong avoidance; blank = absent from vegetation and diet.
Total = relative to proportion in total sward. Surface = relative to proportion at sward surface.

Table 7.6: Selectivity indices for guanaco diets from the Nardus comminuty.

selection for seed/flowerhead did not follow the same pattern.

With the exception of the flowers of *Luzula* spp. grass-like monocotyledonous plants were strongly avoided. In general there was also avoidance of dicotyledonous plants, and where selection for a particular species did occur it was not consistent.

7.2.3 The Calluna community

The mean proportions of components in the diet consumed by the guanacos on each occasion are tabulated and depicted in Table 7.7 and Figure 7.3 respectively.

Despite *Calluna vulgaris* dominating the dwarf-shrub community this species played a minor role in the diet selected by the camelids. Of the different morphological units available green shoots made the greatest contribution yet never accounted for more than 12 per cent of the material consumed. The other heath species available made even less impact and were all but omitted from the diet. Green and dead leaves of *Vaccinium myrtillus* made a consistent contribution (Table 7.8) yet *Vaccinium vitis-idaea* leaves never accounted for more than one per cent.

Despite the low availability of grass species on the heather community these accounted for the bulk of the diet selected. In particular over 30 per cent of the material consumed on each occasion was green lamina of *Festuca ovina*. Dead lamina of *Festuca ovina* also made a substantial, if variable, contribution to the diet selected. In contrast both green and dead lamina of *Deschampsia flexuosa* were generally avoided.

Although grass-like monocotyledonous plants had been disregarded on the indigenous grassland, they made a contribution to each of the diets selected from the dwarf-shrub community reflecting the lack of preferred plant species. The inclusion of *Carex* spp. occurred despite this category never featuring in the vegetation data, nor the diets of

Vegetation category			Summer 1991	Spring 1992	Summer 1992
Calluna	shoot	green	3.7 ± 0.82	8.1 ± 3.29	11.6 ± 4.49
		dead	1.1 ± 0.64	2.5 ± 1.31	2.7 ± 1.00
	wood		0.6 ± 0.47	0.6 ± 0.35	2.3 ± 0.56
	flower		2.1 ± 0.97	0.1 ± 0.07	8.8 ± 3.58
Erica	shoot	green	0	0.2 ± 0.20	1.0 ± 0.68
		dead	0	-	0.0 ± 0.04
	wood		0	-	0
	flower		0	-	0.1 ± 0.15
Empetrum			0	0	0
V. myrtillus	leaf	green	3.3 ± 2.07	13.7 ± 4.11	5.1 ± 1.33
		dead	2.3 ± 0.96	4.8 ± 1.15	2.7 ± 1.56
V. vitis-idaea	leaf	green	0	0	0.8 ± 0.73
		dead	0	0.3 ± 0.34	0.3 ± 0.24
Vaccinium	stem	green	2.2 ± 1.39	3.5 ± 1.04	4.8 ± 2.10
		dead	0.8 ± 0.51	0.1 ± 0.07	0.5 ± 0.31
Festuca	leaf	green	31.1 ± 16.40	34.2 ± 5.44	33.8 ± 5.06
		dead	13.1 ± 3.64	5.1 ± 0.77	18.0 ± 3.00
Deschampsia	leaf	green	0	0.0 ± 0.03	0.7 ± 0.07
		dead	0	0.0 ± 0.03	0
broad-leaved grass	leaf	green	15.0 ± 12.64	4.2 ± 1.29	1.9 ± 0.80
		dead	11.2 ± 7.16	1.7 ± 0.57	1.7 ± 0.48
grass vegetative stem			4.1 ± 4.11	2.9 ± 1.15	0.9 ± 0.32
grass flower stem			0.3 ± 0.25	4.7 ± 0.69	1.9 ± 1.17
grass seed/flowerhead			0.1 ± 0.08	1.2 ± 0.52	-
Juncus		green	-	9.0 ± 5.18	0.5 ± 0.30
		dead	-	2.7 ± 1.49	0.4 ± 0.24
Carex		green	2.2 ± 2.22	0.2 ± 0.17	-
		dead	5.9 ± 5.91	-	-
Galium		green	0.2 ± 0.08	0.0 ± 0.03	0
		dead	0.1 ± 0.08	0.1 ± 0.07	-
moss			0.7 ± 0.67	0.1 ± 0.10	0.0 ± 0.03
			n = 3	n = 10	n = 9

0 = recorded in vegetation but not in diet. - = absent from vegetation and diet.
All results expressed as mean percentage ± s.e.m.

Table 7.7: Composition of the diets consumed by the guanacos on the Calluna community.

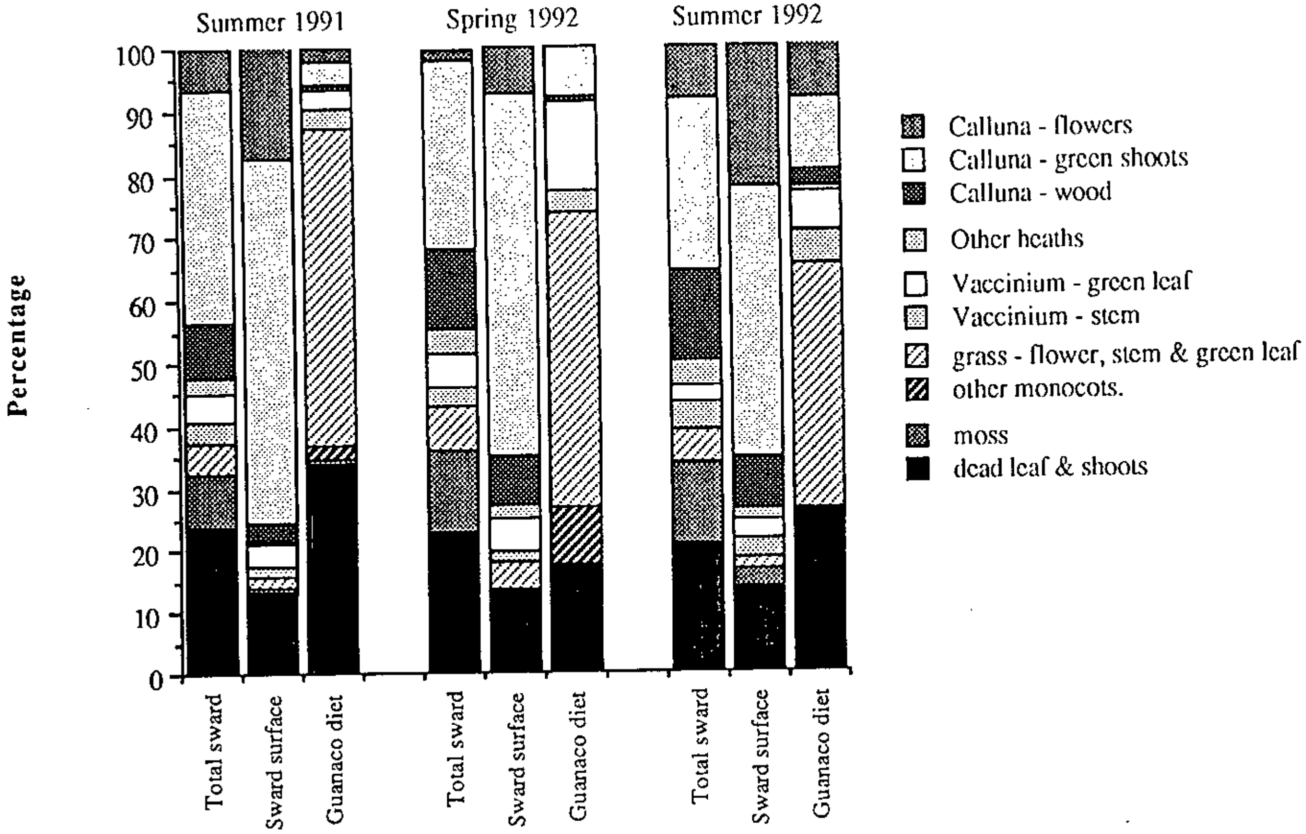


Figure 7.3: Composition of the diets consumed by the guanacos on the Calluna community.

Vegetation category			Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992	
Calluna	shoot	green	ns	ns	ns	
		dead	ns	ns	ns	
	wood		ns	*	**	
	flower		ns	ns	**	
Erica	shoot	green	ns	ns	ns	
		dead	ns	ns	ns	
	flower		ns	ns	ns	
V. myrtillus	leaf	green	ns	ns	ns	
		dead	*	ns	ns	ψ
V. vitis-idaea	leaf	green	ns	ns	ns	
		dead	ns	ns	ns	
Vaccinium	stem	green	ns	ns	ns	
		dead	*	ns	*	$\phi\psi$
Festuca	leaf	green	ns	ns	ns	ψ
		dead	ns	ns	***	
Deschampsia	leaf	green	ns	ns	ns	
		dead	ns	ns	ns	
broad-leaved grass	leaf	green	ns	*	ns	ψ
		dead	*	*	ns	
grass vegetative stem			**	ns	***	
grass flower stem			*	ns	*	$\phi\psi$
grass seed/flowerhead			ns	ns	ns	
Juncus		green	ns	ns	ns	
		dead	ns	ns	ns	
Carex		green	**	***	ns	$\phi\psi$
		dead	ns	ns	ns	
Galium	all	green	**	**	ns	
		dead	ns	ns	ns	
moss			ns	ns	ns	ϕ

ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$

ϕ = plot effect

ψ = plot x session interaction

Table 7.8: Summary of statistical analysis comparing the diets selected by the guanacos from the Calluna community during each experimental session

either of the other two species of animal studied. The contributions of forbs such as *Galium saxatile* and moss remained small.

The Electivity Index values for the components in the diets consumed by the camelids on the Calluna community are listed in Table 7.9. Overall the response of the camelids to the various vegetation categories was unaffected by seasonal changes in availability. In general there was strong avoidance of all parts of *Calluna vulgaris*. In contrast the response to morphological units of *Erica* spp. was mixed. Green leaves of *Vaccinium myrtillus* were tolerated or weakly avoided yet dead leaves highly selected. Likewise, selection for dead leaves of *Vaccinium vitis-idaea* was more consistent than selection of green leaves. There was relatively consistent weak selection for green *Vaccinium* spp. stem while the response to dead stem varied from strong avoidance to weak selection. In general with the exception of lamina of *Deschampsia flexuosa* there was strong selection for morphological units of graminoid species and grass-like monocotyledonous plants irrespective of state.

7.3 DIET DIGESTIBILITY

7.3.1 *In vitro* digestibility

The mean digestibility of the diets selected from each community by the oesophageal fistulated animals during each experimental session are listed in Table 7.10a and plotted in Figure 7.4a . Summaries of statistically significant differences are given in Table 7.10b and 7.10c.

There were no significant difference between the digestibility of the diet selected on each occasion from the Lolium sward. On the Nardus grassland the digestibility of the diet selected in summer 1992 was significantly lower than that selected during the previous spring session. Similarly the diet selected from the Calluna community during the spring experimental session had a significantly higher digestibility than that consumed

Vegetation category			Summer 1991		Spring 1992		Summer 1992	
			Total	Surface	Total	Surface	Total	Surface
Calluna	shoot	green	- -	- -	- -	- -	-	- -
		dead	- -	- -	- -	- -	- -	- -
	wood		- -	- -	- -	- -	- -	- -
	flower		- -	- -	- -	- -	0	-
Erica	shoot	green	- -		0	+ +	+	+
		dead	- -				0	+ +
	wood		- -				- -	
	flower		- -				+ +	+ +
Empetrum			- -	- -	- -	- -	- -	- -
V. myrtillus	leaf	green	0	0	+ +	+	+	+
		dead	+ +	+ +	+ +	+ +	+ +	+ +
	flower							
V. vitis-idaea	leaf	green	- -		- -	- -	+	+ +
		dead	- -		+ +	+ +	+ +	+ +
Vaccinium	stem	green	-	+	+	+	+	+
		dead	0	+	- -	- -	-	+
Festuca	leaf	green	+ +	+ +	+ +	+ +	+ +	+ +
		dead	+ +	+ +	+ +	+ +	+ +	+ +
Deschampsia	leaf	green	- -	- -	- -	- -	- -	-
		dead	- -	- -	- -	- -	- -	- -
broad-leaf	leaf	green	+ +	+ +	+ +	+ +	+ +	+ +
		dead	+ +	+ +	+ +	+ +	+ +	+ +
vegetative stem			- -	+ +	+	+ +	0	+ +
flower stem			+ +	+ +	+ +	+ +	+ +	+ +
seed/flowerhead			+ +	-	+ +	+ +		
Juncus		green			+ +	+ +	+	+ +
		dead			+ +	+ +	+ +	+ +
Carex			+ +	+ +	+ +	+ +		
				+ +				
Galium		green	+	+ +	+ +	+ +	- -	
		dead	-	+ +	0	+ +		
moss			- -	-	- -	- -	- -	- -

Abbreviations: + + = strong selection; + = weak selection; 0 = indifference; - = weak avoidance; - - = strong avoidance; blank = absent from vegetation and diet.
Total = relative to proportion in total sward. Surface = relative to proportion at sward surface.

Table 7.9: Selectivity indices for guanaco diets from the Calluna community.

a.

Vegetation	**Summer 1991**	**Spring 1992**	**Summer 1992**
Lolium	0.766 ± 0.0093	0.801 ± 0.0079	0.788 ± 0.0239
Nardus	0.642 ± 0.0263	0.694 ± 0.0111	0.596 ± 0.0152
Calluna	0.491 ± 0.0568	0.612 ± 0.0178	0.508 ± 0.0288

b.

Vegetation	**Summer 1991 v. Spring 1992**	**Summer 1991 v. Summer 1992**	**Spring 1992 v. Summer 1992**
Lolium	ns	ns	ns
Nardus	ns	ns	**
Calluna	***	ns	***

c.

Session	**Lolium v. Nardus**	**Lolium v. Calluna**	**Nardus v. Calluna**
Summer 1991	*	**	*
Spring 1992	***	***	**
Summer 1992	***	***	***

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 7.10: *In vitro* digestibility of diets selected by guanacos.

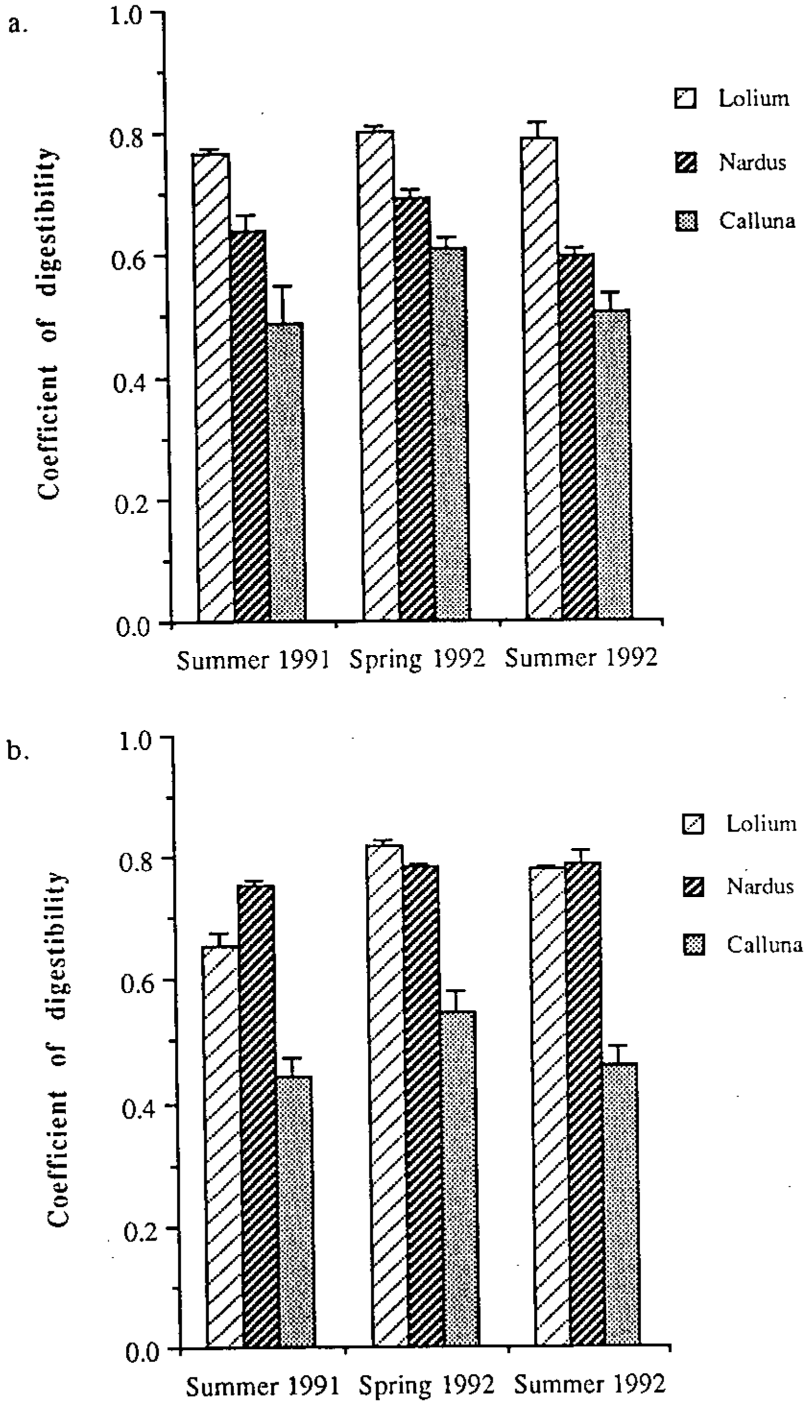


Figure 7.4: Effect of season and vegetation type on digestibility of diets selected by guanacos as determined using: a. *in vitro* analysis; b. n-alkane analysis.

during either of the summer sessions.

Within each experimental session there were significant differences in digestibility between the diets selected on each of the three vegetation types. The digestibility of the diet consumed on the Lolium sward was always higher than that of the diets selected on either indigenous community; and the digestibility of the diets from the indigenous grassland were consistently higher than those from the dwarf-shrub community.

7.3.2 Digestibility from n-alkanes

Equivalent results and statistical information for diet digestibility as determined using the n-alkane technique have been plotted and tabulated in Figure 7.4b and Table 7.11a, 7.11b and 7.11c respectively.

The digestibility of the diet selected from the Lolium sward in summer 1991 was significantly lower than that of the diets consumed in either session in 1992. No differences between sessions were recorded in the digestibility of the diets from the indigenous grassland. In contrast there was a seasonal difference in the diets selected from the dwarf-shrub community with the digestibility of that consumed in spring 1992 significantly higher then that of either summer session.

While the digestibility of the diet selected from the Calluna community was consistently lower than that from either grassland community, only during the summer 1991 experimental session was there a difference between the digestibility of the diets consumed on the Lolium and Nardus swards, with that of the Nardus diet lower.

7.4 INTAKE

7.4.1 Organic matter intake

The organic matter intakes (OMI) of the guanacos on each community during each experimental session are listed in Table 7.12a and plotted in Figure 7.5a. Statistical

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	0.654 ± 0.0221	0.820 ± 0.0088	0.779 ± 0.0045
Nardus	0.752 ± 0.0120	0.783 ± 0.0055	0.786 ± 0.0243
Calluna	0.440 ± 0.0326	0.546 ± 0.0321	0.460 ± 0.0281

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	*	ns	ns
Nardus	ns	ns	ns
Calluna	**	ns	*

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	ns	***	***
Spring 1992	ns	***	***
Summer 1992	ns	***	***

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 7.11: Digestibility of diets selected by guanacos as determined using n-alkanes.

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	1.137 ± 0.0896	2.486 ± 0.3047	1.897 ± 0.1010
Nardus	1.973 ± 0.1976	2.617 ± 0.1340	2.756 ± 0.3750
Calluna	0.970 ± 0.0310	1.322 ± 0.0763	0.820 ± 0.0463

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	**	*	ns
Nardus	ns	*	ns
Calluna	ns	ns	ns

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	*	ns	**
Spring 1992	ns	**	**
Summer 1992	*	*	***

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 7.12: Organic matter intake of guanacos (kg/day).

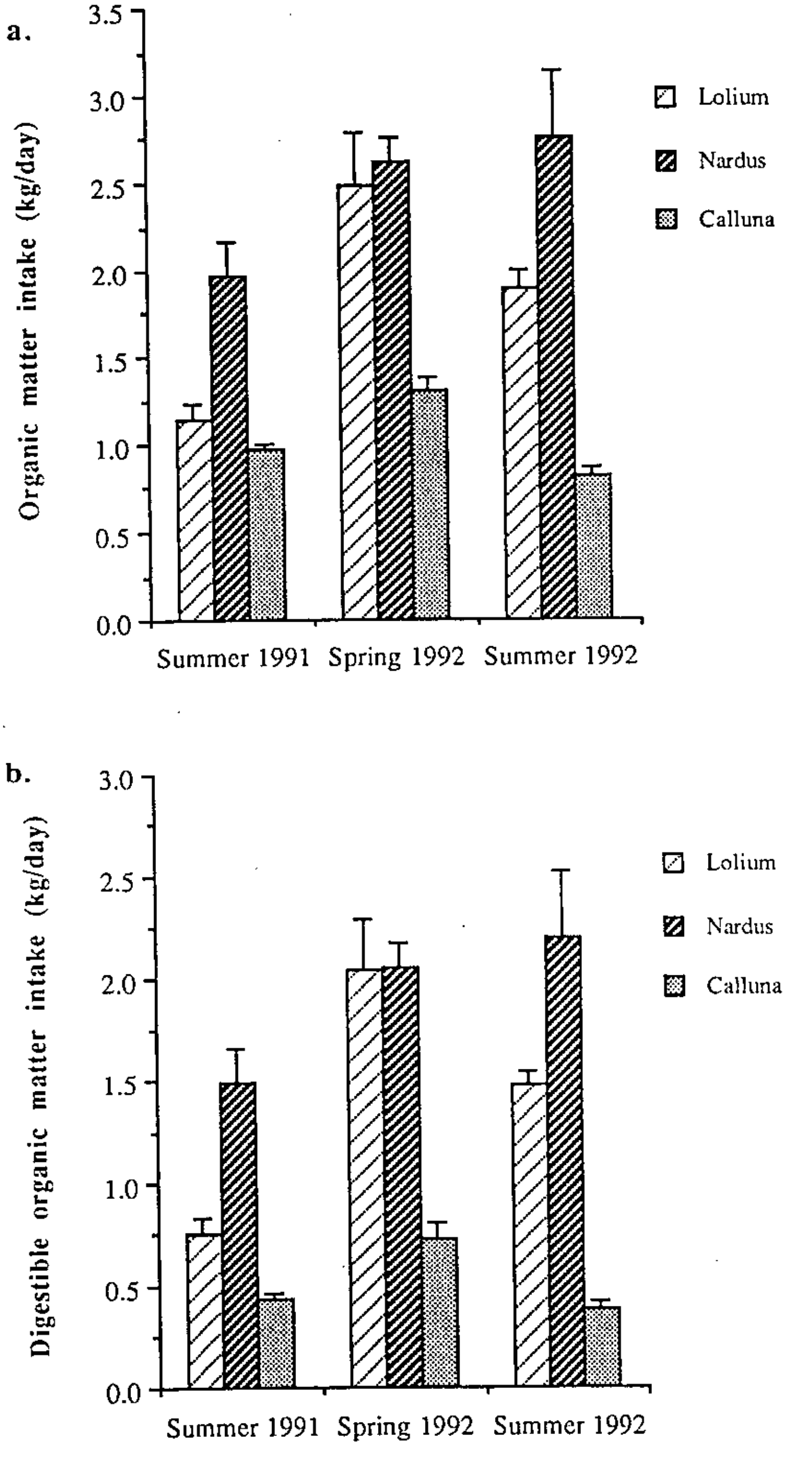


Figure 7.5: Effect of season and vegetation type on: a. organic matter intake; and b. digestible organic matter intake of guanacos (kg/day).

differences are summarised in Table 7.12b and 7.12c. The OMI of the guanacos on the Lolium sward was significantly lower during summer 1991 than either session in 1992. Likewise the OMI on the Nardus sward was significantly higher in summer 1992 than summer 1991. There were no differences between sessions in the amount consumed on the dwarf-shrub community.

During the experimental periods in 1991 the OMI of the guanacos was significantly higher on the Nardus grassland than on either the Lolium or Calluna communities. In spring 1992 OMI was similar on the grassland communities but significantly lower on the dwarf-shrub community. This lower OMI on the Calluna community was maintained during summer 1992 when there was also a significant difference between the Lolium and Nardus swards, with that on the Nardus sward highest.

7.4.2 Digestible organic matter intake

The digestible organic matter intakes (DOMI) of the guanacos on each community during each session are listed in Table 7.13a and plotted in Figure 7.5b. Statistical differences are summarised in Table 7.13b and 7.13c.

The DOMI on the sown sward was significantly higher during the spring session than during either summer session, and higher in summer 1992 than summer 1991. In contrast, no seasonal differences in DOMI were recorded on either indigenous community. However, the DOMI value for summer 1991 on the Nardus community was significantly lower than that recorded in summer 1992.

During summer 1991 session DOMI was significantly higher on the Nardus sward than on either the Lolium or Calluna communities. In spring, however, DOMI on the grassland communities was similar, and significantly higher than that on the dwarf-shrub community. During summer 1992 the higher DOMI on the grassland communities was

a.

Vegetation	**Summer 1991**	**Spring 1992**	**Summer 1992**
Lolium	0.750 ± 0.0785	2.038 ± 0.2533	1.477 ± 0.0735
Nardus	1.490 ± 0.1713	2.050 ± 0.1129	2.193 ± 0.3324
Calluna	0.425 ± 0.0268	0.728 ± 0.0739	0.381 ± 0.0385

b.

Vegetation	**Summer 1991 v. Spring 1992**	**Summer 1991 v. Summer 1992**	**Spring 1992 v. Summer 1992**
Lolium	***	*	*
Nardus	ns	*	ns
Calluna	ns	ns	ns

c.

Session	**Lolium v. Nardus**	**Lolium v. Calluna**	**Nardus v. Calluna**
Summer 1991	*	ns	**
Spring 1992	ns	***	**
Summer 1992	*	**	***

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 7.13: Digestible organic matter intake of guanacos (kg/day).

maintained, with a significantly higher DOMI on the indigenous sward in comparison with the sown sward also recorded.

7.5 GRAZING PATTERN

7.5.1 Total grazing time

The total grazing time of the guanacos on each community during each experimental session are listed in Table 7.14a and plotted in Figure 7.6. Statistical differences are summarised in Table 7.14b and 7.14c.

The total grazing time of the guanacos was significantly higher when grazing the Lolium sward in summer 1992 than it had been during either of the previous experimental periods. The grazing time on the Nardus community in summer 1992 was significantly lower than that recorded during summer 1991 or spring 1992. The grazing times for each experimental period on the Calluna community were similar.

During the summer 1991 and spring 1992 experimental sessions no significant differences between grazing times on the three vegetation types were recorded. However, in summer 1992 the grazing time on the Lolium sward was significantly higher than that recorded when the guanacos were grazing on either of the indigenous communities.

7.5.2 Grazing pattern

The grazing pattern of the guanacos on each occasion was also discerned from the vibracorder data. As the results from all three sessions were similar only summer 1991 has been plotted as an example. Figure 7.7 shows the cumulative results for each measurement week, and illustrates that grazing was predominately confined to daylight hours and that the pattern of grazing was unaffected by vegetation type.

a.

Vegetation	Summer 1991	Spring 1992	Summer 1992
Lolium	542 ± 22.4	592 ± 54.5	698 ± 24.7
Nardus	562 ± 24.1	628 ± 37.2	492 ± 25.6
Calluna	556 ± 13.2	581 ± 39.8	528 ± 38.3

b.

Vegetation	Summer 1991 v. Spring 1992	Summer 1991 v. Summer 1992	Spring 1992 v. Summer 1992
Lolium	ns	***	*
Nardus	ns	ns	**
Calluna	ns	ns	ns

c.

Session	Lolium v. Nardus	Lolium v. Calluna	Nardus v. Calluna
Summer 1991	ns	ns	ns
Spring 1992	ns	ns	ns
Summer 1992	***	***	ns

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites

Table 7.14: Total grazing time of guanacos (min/day).

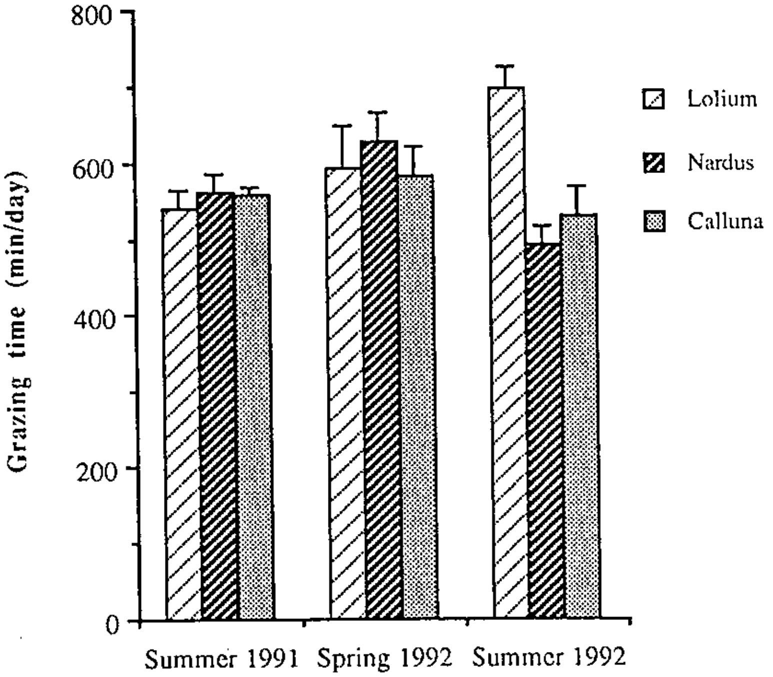
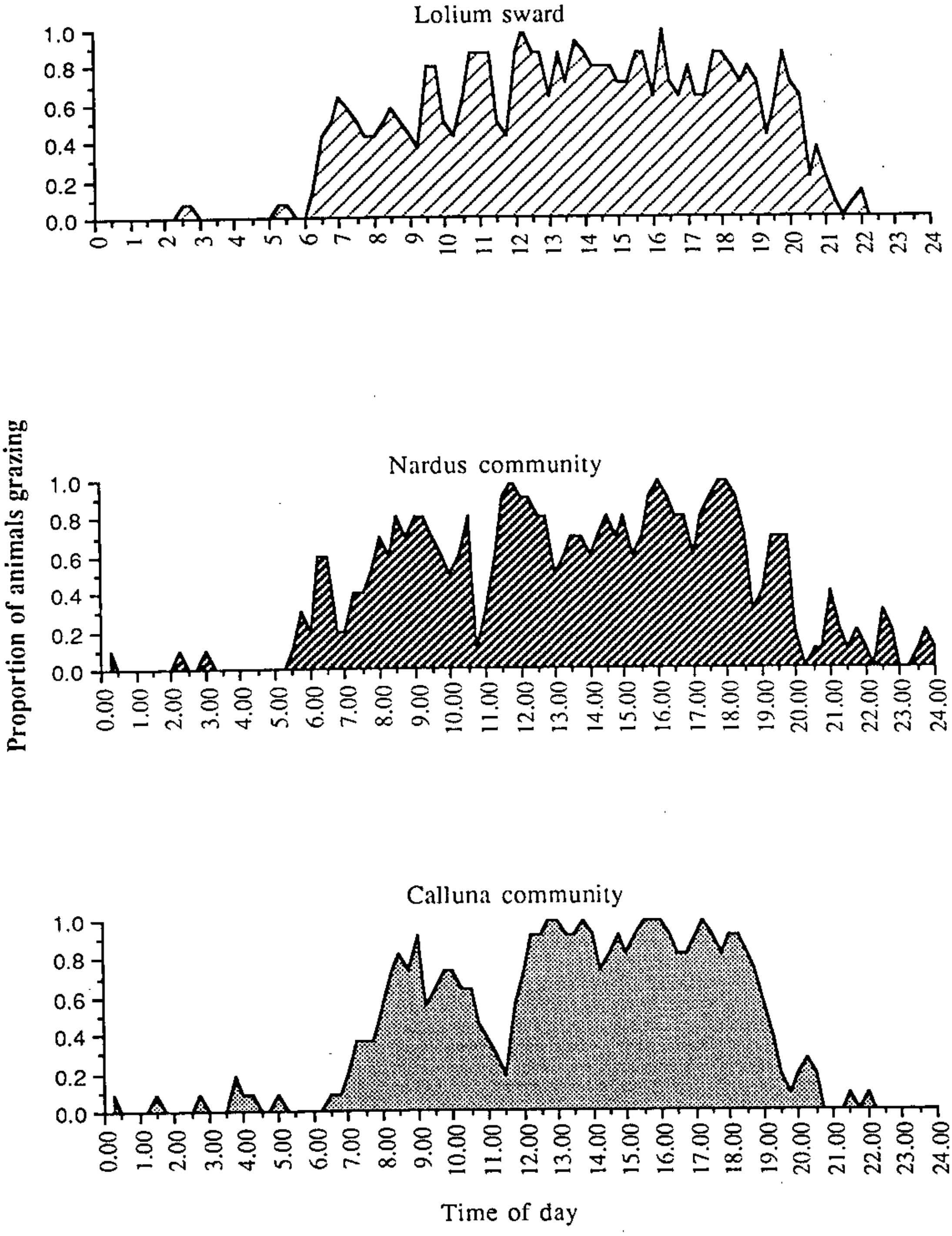


Figure 7.6: Effect of season and vegetation type on total grazing time of guanacos



Lolium sward

Nardus community

Calluna community

Figure 7.7:Effect of season and vegetation type on grazing pattern of guanacos.

7.5.3 Synchronisation of grazing

Table 7.15 gives the kappa coefficients of synchronisation (K) of grazing, not grazing and overall activity, together with the variance and z statistics for each K. All K's were significantly different from zero indicating that synchronisation of activity was greater than would be expected by chance. On each occasion the camelids were less synchronised when grazing than when not grazing. There was no consistent order within sessions to the K value for overall activity calculated for each vegetation type.

7.5.4 Bite rate

The bite rates for the guanacos on each community during each experimental session are listed in Table 7.16a and plotted in Figure 7.8. Statistical differences are summarised in Table 7.16b and 7.16c.

The bite rate of the camelids on the sown sward in summer 1992 was significantly higher than it had been during either of the two previous sessions on the same sward. The only other significant difference between sessions was a lower bite rate on the Nardus sward in summer 1991 in comparison with spring 1992.

During summer 1991 and spring 1992 the bite rates of the guanacos on each of the three vegetation communities were similar. However, in summer 1992 the bite rate on the sown sward was recorded as being significantly higher than that on the indigenous grassland community.

7.6 DISCUSSION

Initially only one oesophageal fistulated guanaco was prepared as the feasibility of creating and maintaining surgically-altered animals of this species was unknown. The surgical procedure adopted differed in detail from the technique in other ruminants due to the anatomy of the guanaco neck (Goddard and Fraser, 1994). As complete eversion

		Grazing			Not grazing			Total		
Session	Vegetation	K	Var (K)	z	K	Var (K)	z	K	Var (K)	z
Summer 1991	Lolium	0.105	0.0001428	8.80	0.140	0.0005808	5.82	0.372	0.0002081	25.77
	Nardus	0.139	0.0006682	5.37	0.167	0.0015815	4.20	0.461	0.0012023	13.28
	Calluna	0.190	0.0003054	10.86	0.188	0.0002927	11.00	0.567	0.0000869	60.84
Spring 1992	Lolium	0.124	0.0002692	7.58	0.158	0.0008445	5.42	0.426	0.0003631	22.35
	Nardus	0.159	0.0004478	7.51	0.181	0.0008456	6.24	0.512	0.0004235	24.86
	Calluna	0.117	0.0001087	11.24	0.173	0.0007182	6.45	0.443	0.0003083	25.21
Summer 1992	Lolium	0.159	0.0002225	10.69	0.209	0.0008228	7.28	0.558	0.0003454	30.00
	Nardus	0.140	0.0002592	8.72	0.170	0.0007241	6.45	0.470	0.0002852	28.02
	Calluna	0.169	0.0002345	11.03	0.226	0.0009469	7.33	0.598	0.0004285	28.87

K = kappa coefficient of synchronisation
Var(K) = variance of K
z = z statistic for K

Table 7.15: Grazing synchronisation of guanacos

a.

Vegetation	**Summer 1991**	**Spring 1992**	**Summer 1992**
Lolium	37.7 ± 3.34	39.6 ± 3.81	56.0 ± 2.03
Nardus	33.1 ± 3.05	44.9 ± 1.85	39.0 ± 1.56
Calluna	37.0 ± 2.80	36.1 ± 3.21	41.9 ± 1.50

b.

Vegetation	**Summer 1991 v. Spring 1992**	**Summer 1991 v. Summer 1992**	**Spring 1992 v. Summer 1992**
Lolium	ns	***	***
Nardus	*	ns	ns
Calluna	ns	ns	ns

c.

Session	**Lolium v. Nardus**	**Lolium v. Calluna**	**Nardus v. Calluna**
Summer 1991	ns	ns	ns
Spring 1992	ns	ns	ns
Summer 1992	***	ns	ns

a. mean ± s.e.m.
b. summary of statistical differences between sessions
c. summary of statistical differences between vegetation communitites
ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$

Table 7.15: Bite rates of guanacos (bites/min).

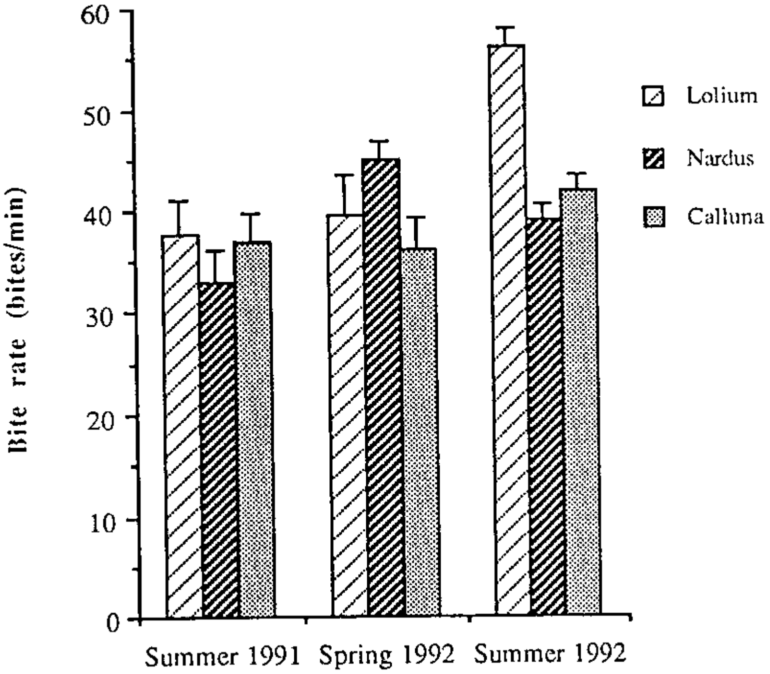


Figure 7.8: Effect of season and vegetation type on bite rate of guanacos.

of the oesophageal wall is not possible, healing was found to take longer than in ruminants. Consequently a recovery period of at least ten weeks is necessary before the fistula stabilises and extrusa collection is feasible. It was therefore not practicable to proceed with further preparations in 1991.

As samples were collected from only one animal in 1991 the corresponding diet composition and *in vitro* digestibility data must be considered with care. These samples were also used to describe the n-alkane content of the diet and hence intake and digestibility estimated made in 1991 may be biased. However, comparison with the equivalent data collected in 1992 when five oesophageal fistulates were available indicated that in general the results from the first year were similar to those obtained in 1992. Thus the inclusion of C_{33}-alkane contributions derived from analysis of the few extrusa samples obtained in 1991 is probably preferable to using herbage samples and attempting to predict diet composition on structurally complex heterogeneous vegetation.

Initially herbage intake from each of the three vegetation types was calculated using the ratio C_{33}:C_{32}-alkane as described in Chapter Four. Diet digestibility was then determined using these results and the ratio of faecal and dosed C_{36}-alkane. When the guanacos had been grazing either grassland community this approach produced realistic intake results together with digestibility coefficients consistent with those obtained from *in vitro* analysis of the extrusa samples. In contrast, the results for both intake and diet digestibility on the dwarf-shrub community were inexplicably low. On all three occasions intake was calculated as less than 0.8 kgOM/day (summer 1991 = 0.79 $\pm$ 0.063: spring 1992 = 0.75 $\pm$ 0.065: summer 1992 = 0.54 $\pm$ 0.043) with the corresponding coefficients of organic matter digestibility of less than 0.30 (summer 1991 = 0.294 $\pm$ 0.0794: spring 1992 = 0.185 $\pm$ 0.0735: summer 1992 = 0.174 $\pm$ 0.0483).

Subsequent inquiries revealed that even when allowances were made for the small amounts of degradation of long-chain alkanes that occur during the digestive process, the percentage contribution of C_{33}-alkane to the overall alkane concentration was significantly higher in the extrusa samples than in the faeces samples from either the oesophageal fistulated or intact grazing animals. Thus, although the long-term diet of the fistulates was similar to that of the intact grazing animals, during the comparatively short periods of extrusa collection they were selecting unrepresentatively high quantities of a plant containing high levels of C_{33}-alkane, i.e. *Calluna vulgaris* (R.W. Mayes, unpublished data). Consequently the proportions of *Calluna vulgaris* recorded during the microscopic examination of the diets selected during each experimental session will be overestimations of the contribution of this species to the guanacos' diet.

In addition to highlighting this disparity between the C_{33}-alkane levels, comparison of the percentage contribution of each odd-chain alkanes between C_{29}-alkane and C_{35}-alkane to their total concentration revealed that the extrusa levels of C_{31}-alkane would be a more representative alternative to C_{33}-alkane for inclusion in the intake equation since the proportions matched those found in the faeces samples. Unlike C_{33}-alkane this alkane is not found in extreme concentrations in any one of the plant species recorded as present on the Calluna community (R.W. Mayes, unpublished data). Thus intake on the dwarf-shrub community was recalculated using the ratio of C_{31}:C_{32}-alkane. This increased the organic matter intake by up to 0.5 kg/day (spring 1992) and brought the diet digestibility coefficients much closer to those estimated using the *in vitro* method and hence, these results are quoted in the results section.

The intake values are higher than those estimated for housed llama x guanaco crossbreds (Warmington, Wilson and Barry, 1989) and free-ranging llamas (Farfan *et al.*, 1986). In general, intake was higher on the grass swards than on the dwarf-shrub community.

Although no difference was recorded between the intake on the sown and indigenous grassland during the spring session, during both summer sessions intake was higher on the indigenous community. This is despite *in vitro* digestibility of the diets selected from the Lolium sward being significantly higher than those consumed on the Nardus community. Similar findings for the two domesticated species of South American camelid have also been reported. For example, the intake of llamas under range conditions has been found to be lower during the rainy season (Farfan *et al.*, 1986) yet diet digestibility was higher during the rainy season than during the dry months (Fierro *et al.*, 1986). Similarly, organic matter intake of free-ranging alpacas was found to be greater during the dry season than the wet season when the *in vitro* digestibility of the diet selected was significantly higher (Reiner *et al.*, 1987).

The differences in herbage intake recorded on the three vegetation types did not correspond to differences in grazing time. Indeed the total amount of time spent grazing by the guanacos was relatively constant on all three vegetation communities. This implies that the guanacos responded to the different vegetation types by adjusting either the amount of material prehended in each bite and/or the proportion of time spent selecting the next bite. Thus differences in organic matter intake would appear to be the result of changes in ingestive behaviour rather than a response to the nutritive properties of the vegetation being consumed.

The vibracorder traces created by the guanacos were different from those generated by either the goats or the red deer. Irrespective of vegetation type activity registered as a fragmented line of inconsistent intensity instead of the distinct dark band which normally indicates grazing in other species (Hodgson, 1982b). Observations in the field suggest that the animals were frequently distracted from grazing and tended to integrate this and other behaviours rather than having well-defined grazing bouts. Consequently further studies would be more enlightening if jaw-recorders which captured data on a minute by minute basis were used in place of vibracorders. Unfortunately characteristic activities performed by these animals are not conducive to successful equipment operation. For example, during the current study rolling by the guanacos frequently resulted in failure to obtain a complete vibracorder trace and/or irreparable damage to what was considered a relatively robust mechanism. The diurnal pattern of activity established matches profiles recorded for llamas in southern France (Prud'hon, 1991) and alpacas in Germany (Scheibe *et al.*, 1991).

Despite the relative homogeneity of the established sown sward, the botanical composition of the diets selected by the guanacos was markedly different from that of the herbage on offer. This was primarily related to the camelids strong avoidance of green leaf of clover and other dicotyledonous plants. This avoidance of dicotyledonous plants extended to the forbs encountered on the Nardus community. This agrees with previous work comparing the botanical composition of diets selected from Andean rangeland which identified llamas as consuming small quantities of herbaceous plants relative to alpacas and sheep (Pfister *et al.*, 1989). Elsewhere guanacos have been identified as selecting forbs (Raedeke, 1980). However, during Raedeke's (1980) study only one particular species unavailable on the three vegetation communities of the current study was consumed in substantial quantities.

On the Calluna community the strong and consistent avoidance of the dominant plant species by the guanacos appears to have precipitated a switch to discrimination between dicotyledonous plant species, with selection for *Vaccinium myrtillus*. It is interesting to note that, although the guanacos exhibited an ability to select green *Vaccinium* spp. stem while avoiding dead stem, there was stronger selection for dead *Vaccinium* spp. leaf than green leaf. This, and the selection for dead clover leaf which was also recorded, may be due to unattached dead leaves being inadvertently consumed amongst mouthfuls of grass. Alternatively, chemical characteristics of these plant parts which made them unpalatable to the guanacos when green may be reduced in dead or dying plant parts.

Another example of a change in response to the same plant category on different communities is the switch from avoidance of grass-like monocotyledonous plants on the Nardus grassland to strong selection for these plants on the Calluna community. Sedges and reeds have been found to play a variable role in alpaca diets selected from rangeland depending on season and availability of grass (Reiner and Bryant, 1986). That grasses were the principal food even on the dwarf-shrub community concurs with patterns of forage consumption among free-ranging guanacos in their native habitat (Raedeke, 1980).

Although grazing herbivores generally avoid stem, selection by the guanacos for flowerstem and seed/flowerhead of grasses occurred on all three vegetation types. Free-ranging alpacas have been identified as substituting seeds for stem material during the dry season when forage availability is low (Bryant and Farfan, 1984).

A common pattern of avoidance of vegetative stem relative to the proportion in the sward as a whole but selection relative to the sward surface was found on all three vegetation communities. Thus, although the high proportion of grass seed/flowerhead of grass in the diets suggests that the guanacos were confining their selection to the sward surface, the proportions of vegetative stem indicate that material from the lower strata was also consumed. That discrimination between plant categories was maintained even at the base of the sward is illustrated by avoidance of the moss encountered on both indigenous swards. Thus there was vertical selection within a sward for particular food items in addition to horizontal selection for patches of preferred species.

Clearly the distribution of preferred food items within each of the communities will have influenced the time spent selecting bites. The relatively homogeneous nature of the sown pasture will have resulted in the avoidance of green *Trifolium repens* leaf exhibited being time-consuming. In contrast, the preferred species within the Nardus-dominated community were located together in the inter-tussock areas. Selection of the next bite from a particular patch would require little discrimination making a higher bite rate or larger bites possible without compromising accuracy of selection. Consequently the same herbage intake could be achieved in a shorter time; or alternatively if the grazing time was kept constant as was found intake would be higher.

The species selected by the guanacos from the Calluna community were also patchily distributed, but the distances between patches were much greater and the patch size much smaller than on the indigenous grassland. For example, the Green's Index for *Juncus* spp., which accounted for only per cent of the point quadrat hits, indicate that this vegetation category was highly clumped, yet it was strongly selected by the camelids during all three experimental session. Thus locating the preferred plant species was time consuming yet the quantity of material available was low. This could result in a low bite rate, small bite size and low herbage intake (Spalinger, Hanley and Robbins, 1988) unless grazing time was increased to compensate. Even if the plant parts selected had been of high nutritional value, the high expenditure of time requires in selective feeding generally means that only small bodied and small-mouthed animals with limited rumen capacity can afford to search for disperse high-quality food items (Bell, 1970).

7.7 SUMMARY

1. In general, the guanacos exhibited greater discrimination between plant species than plant parts or state (live or dead).

2. On the established sown sward the guanacos selected graminoid species, while avoiding clover and other dicotyledonous plants.

3. On the indigenous grassland grazing was confined to the inter-tussock areas, and the dominant tussock-grass avoided. Although grass vegetative stem was generally avoided,

grass flowerstem and grass seed/flowerhead were selected.

4. *Calluna vulgaris* was avoided by the guanacos when grazing on the dwarf-shrub community. Graminoid species were instead the main dietary component. Selection for other monocotyledonous plants also occurred, despite these minor components within the sward having a highly clumped distribution.

5. Diet digestibility was primarily dictated by vegetation type. OMI was also influenced strongly by vegetation type, with the intakes on the dwarf-shrub community consistently lowest. Within-session differences in DOMI on the three vegetation types followed the pattern of between-community differences in OMI, indicating that OMI by the guanacos was more variable than their diet digestibility.

6. The guanacos grazed mainly during daylight hours. Their total grazing time and bite rate remained relatively constant irrespective of vegetation type or season.

CHAPTER EIGHT

COMPARISON OF GRAZING ECOLOGY OF GOATS, RED DEER AND SOUTH AMERICAN CAMELIDS

8.1 DIET COMPOSITION

The Spearman's rank coefficients (Table 8.1) indicate that irrespective of vegetation type the diets consumed by the three species of animal were similar.

8.1.1. The Lolium sward

The overall composition of the diets selected by the three species of animal from the sown sward was similar irrespective of season or session (Table 8.1), with the correlation coefficients calculated for the goat/deer comparisons consistently the highest and those for the goat/camelid comparisons lowest.

The composition of the diets consumed by the goats, red deer and guanacos on the Lolium sward on each occasion are compared in Figure 8.1. Table 8.2 summarises between-species differences in the contribution of the various vegetation categories to the diets consumed on each occasion. During the experimental session in 1991 the diets consumed by the three species were similar. The composition of the diets selected by the goats and red deer was also similar during both sessions in 1992. However, there were a number of significant differences between the diet of these two species and that chosen by the guanacos. In general, on each occasion the guanaco diet contained significantly more dead lamina, grass vegetative stem and grass flowerstem while during the spring experimental session it also contained more grass seed/flowerhead. Irrespective of season the camelids consumed significantly less green clover leaf.

8.1.2 The Nardus community.

As was the case for the sown sward, the overall composition of the diets selected by each species of animal from the indigenous grassland was similar (Table 8.1) on all three occasions. However, on this type of vegetation the correlation coefficients of the deer/guanaco comparisons were highest.

Vegetation	Session	G v D	G v C	D v C
Lolium	Summer 1991	0.847	0.829	0.837
	Spring 1992	0.941	0.755	0.811
	Summer 1992	0.871	0.790	0.818
Nardus	Summer 1991	0.774	0.765	0.866
	Spring 1992	0.624	0.648	0.906
	Summer 1992	0.854	0.774	0.974
Calluna	Summer 1991	0.872	0.660	0.645
	Spring 1992	0.857	0.721	0.844
	Summer 1992	0.893	0.844	0.857

G = goat, D = red deer and C = camelid

$p < 0.01$ for all

Table 8.1: Spearman's rank coefficients for comparisons of the diets selected by each species from each vegetation type.

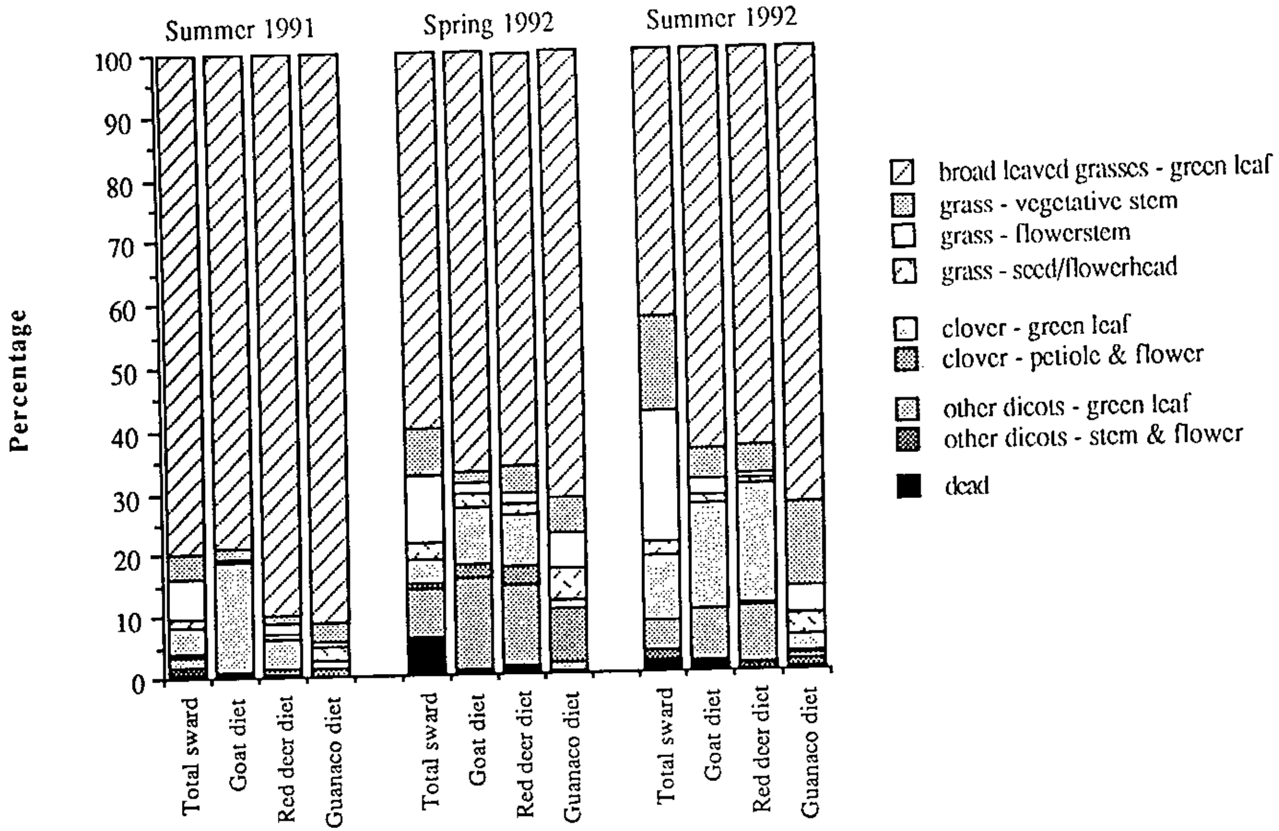


Figure 8.1: Comparison of diet composition of goats, red deer and guanacos on the Lolium sward.

Vegetation category			Summer 1991			Spring 1992			Summer 1992		
			G v. D	G v. C	D v. C	G v. D	G v. C	D v. C	G v. D	G v. C	D v. C
broad-leaf grasses	leaf	green	ns	ns	ns	ns	ns	ns	ns	ns	ns
		dead	ns	ns	ns	*	**	ns	ns	**	**
vegetative stem			ns	ns	ns	ns	**	*	ns	*	**
flowerstem			ns	*	ns	ns	**	*	ns	ns	*
seed/flowerhead			ns	ns	ns	ns	***	**	ns	ns	ns
Trifolium	leaf	green	ns	ns	ns	ns	**	**	ns	*	*
		dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
	petiole		ns	ns	ns	ns	ns	ns	ns	ns	ns
other dicots	leaf	green	ns	ns	ns	ns	ns	ns	ns	ns	*
		dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
	stem		ns	ns	ns	ns	ns	ns	ns	ns	ns
	flower		ns	ns	ns	ns	ns	ns	ns	ns	ns
moss			ns	ns	ns	ns	ns	ns	ns	ns	ns

ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$

Table 8.2: Summary of statistically significant differences in the contribution of vegetation categories to the diets consumed by goats, red deer and guanacos on the Lolium sward.

The composition of the diet consumed by each species of animal from the Nardus community on each occasion is depicted in Figure 8.2. The strong selection by all three species of animal for broad-leaved graminoids growing in the inter-tussock areas is clearly illustrated. The avoidance of *Nardus stricta*, particularly during the summer experimental sessions highlights the increasing unpalatability of this plant as it matures. Although all three species strongly avoided *Nardus stricta* during the summer experimental sessions the goats consumed significantly less of this grass than the deer on both occasions and less than the camelids in summer 1992 (Table 8.3). In general goats also consumed less dead lamina of broad-leaved grasses.

Although statistically significant differences in the proportions of vegetative stem in the diet were identified between all three species over the course of the three experimental sessions, the only diet to contain a significantly different level of grass flowerstem and seed/flowerhead was that of the guanacos in summer 1992. The selection for grass-like monocotyledonous plants by the goats during the spring session was also reflected in significant differences in the proportion of this category in the caprine diet compared with the diets consumed by the red deer and guanacos.

8.1.3 The Calluna community

Once again, the overall composition of the diets selected by each species of animal from the vegetation available was similar (Table 8.1).

That all three species had strongly selected graminoid species is clearly illustrated in Figure 8.3, with the contribution in each case greatest during the spring experimental session. Although consumption of flowers of *Calluna vulgaris* was similar by all three species, during both summer sessions the red deer consumed more green and dead shoots of *Calluna vulgaris* than either the goats or guanacos and more wood of *Calluna vulgaris* than the goats (Table 8.4). In spring, however, the only difference was between

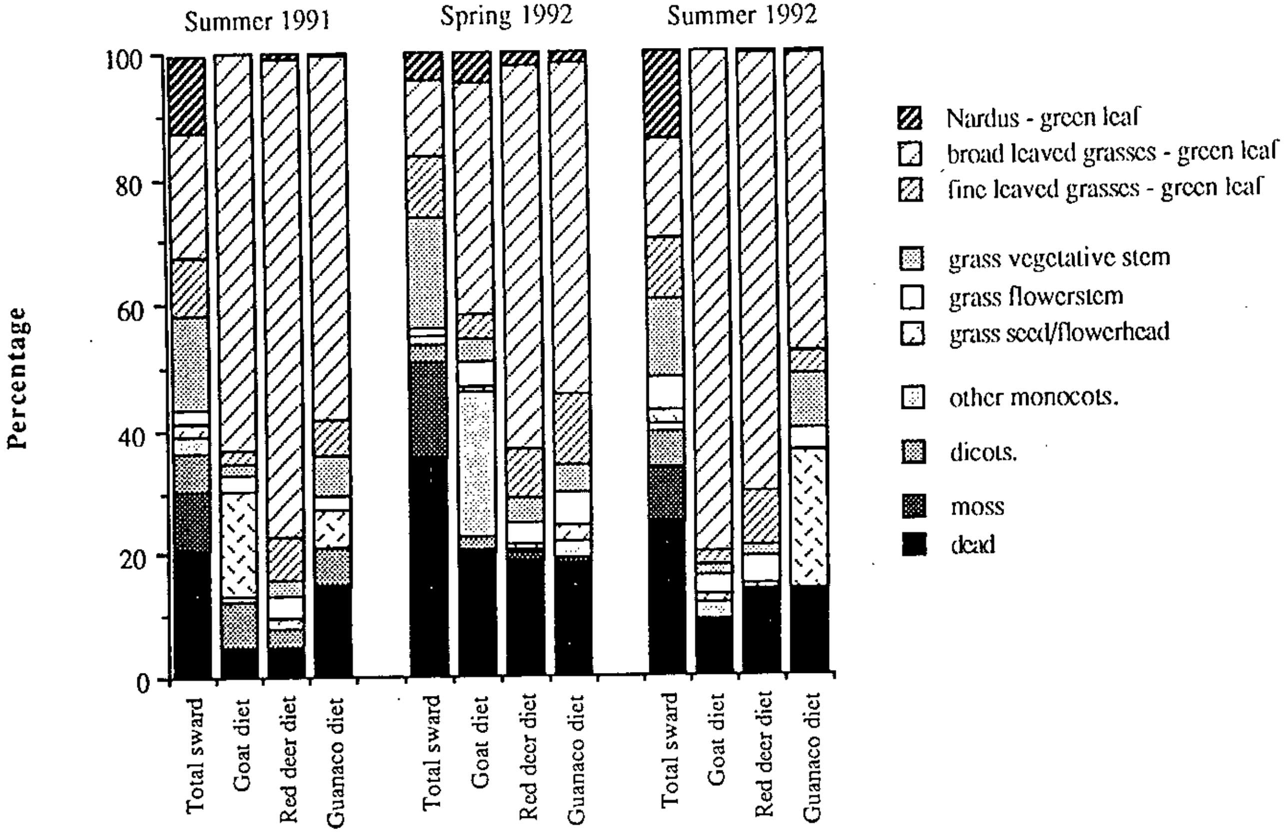


Figure 8.2: Comparison of diet composition of goats, red deer and guanacos on the Nardus community.

Vegetation category		Summer 1991			Spring 1992			Summer 1992		
		G v. D	G v. C	D v. C	G v. D	G v. C	D v. C	G v. D	G v. C	D v. C
Nardus	green	***	ns	ns	ns	ns	ns	**	**	ns
	dead	**	ns	ns	ns	ns	ns	ns	ns	ns
broad-leaved grasses	green	ns	ns	ns	**	ns	ns	ns	***	**
	dead	ns	*	*	**	ns	ns	*	**	ns
Festuca	green	ns	ns	ns	ns	ns	ns	ns	ns	ns
	dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
Deschampsia	green	***	ns	ns	*	**	ns	***	ns	**
	dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
grass vegetative stem		ns	**	*	ns	ns	ns	**	ns	ns
grass flowerstem		ns	ns	ns	ns	ns	ns	ns	**	***
grass seed/flowerhead		ns	ns	ns	ns	ns	ns	ns	***	***
Carex	green	ns	ns	ns	ns	ns	ns	ns	ns	ns
	dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
Luzula	flower	ns	ns	ns	ns	ns	ns	ns	ns	ns
	green	ns	ns	ns	**	*	ns	ns	ns	ns
	dead	ns	ns	ns	**	*	ns	ns	ns	ns
other monocots.	green	ns	ns	ns	ns	ns	ns	ns	ns	ns
	dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
Galium	grean	ns	ns	ns	ns	ns	ns	ns	ns	ns
	dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
Vaccinium	green	ns	ns	ns	ns	ns	ns	ns	ns	ns
	dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
Potentilla	green	ns	ns	ns	ns	ns	ns	ns	ns	ns
	dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
Campanula	green	ns	ns	ns	ns	ns	ns	ns	ns	ns
other dicots.	green	ns	ns	ns	ns	ns	ns	ns	ns	ns
moss		ns	ns	ns	ns	ns	ns	ns	ns	ns

G = goat; D = red deer; C = guanaco
ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Table 8.3: Summary of statistically significant differences in the contribution of vegetation categories to the diets consumed by goats, red deer and guanacos on the Nardus community.

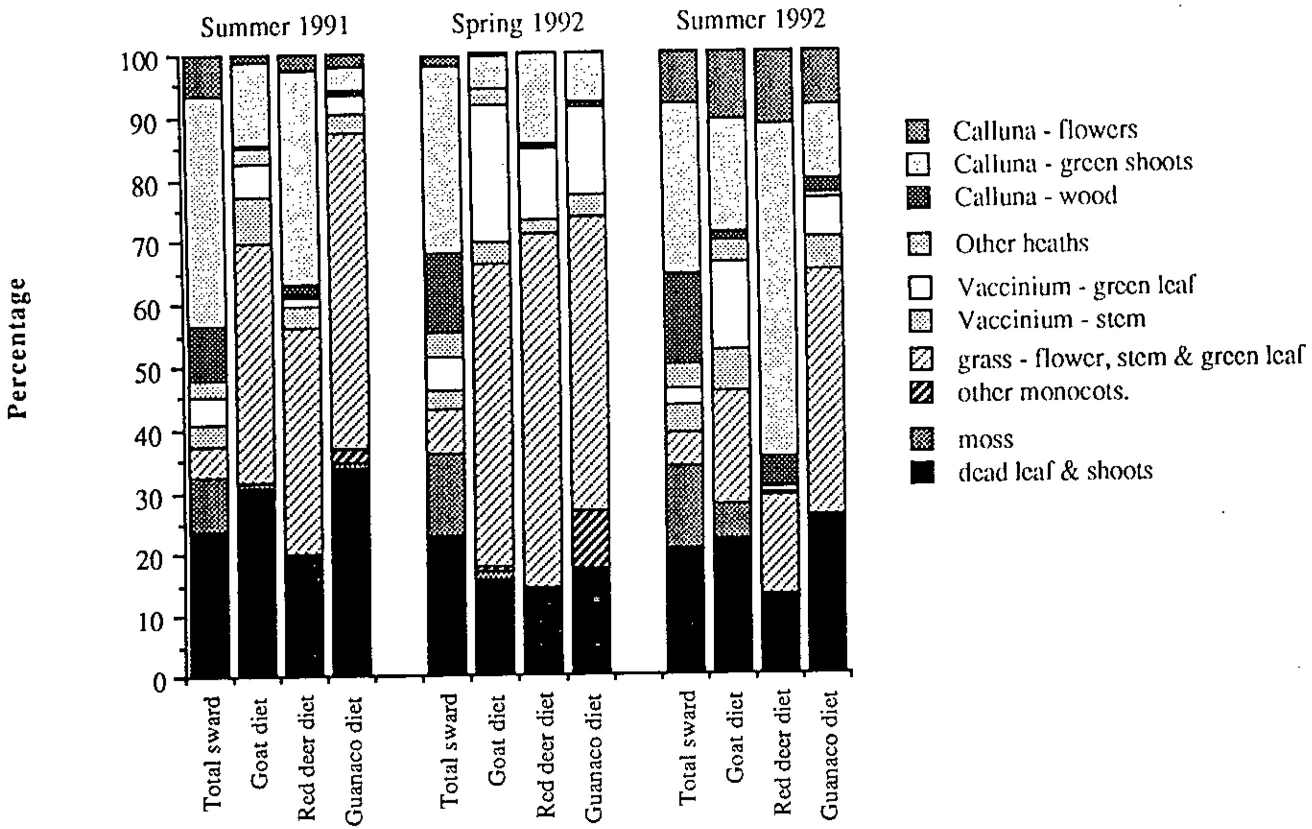


Figure 8.3: Comparison of diet composition of goats, red deer and guanacos on the Calluna community.

Vegetation category		Summer 1991			Spring 1992			Summer 1992		
		G v. D	G v. C	D v. C	G v. D	G v. C	D v. C	G v. D	G v. C	D v. C
Calluna	green	*	ns	*	*	ns	ns	***	ns	***
	dead	**	ns	*	ns	ns	ns	**	ns	*
	wood	*	ns	ns	ns	ns	ns	***	ns	ns
	flower	ns	ns	ns	*	*	ns	ns	ns	ns
Erica	green	ns	ns	ns	ns	ns	ns	*	ns	ns
	dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
	wood	ns	ns	ns	ns	ns	ns	ns	ns	ns
	flower	ns	ns	ns	ns	ns	ns	ns	ns	ns
Empetrum		ns	ns	ns	ns	ns	ns	ns	ns	ns
V. myrtillus	green	ns	ns	ns	ns	ns	ns	***	ns	ns
	dead	*	ns	ns	ns	ns	ns	**	*	ns
	flower	ns	ns	ns	ns	ns	ns	ns	ns	ns
V. vitis-idaea	green	ns	ns	ns	ns	ns	ns	ns	ns	ns
	dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
stem	green	ns	ns	ns	ns	ns	ns	**	ns	*
	dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
Festuca	green	ns	ns	ns	*	ns	ns	ns	*	*
	dead	ns	ns	ns	ns	ns	ns	ns	*	*
Deschmapsia	green	ns	ns	ns	ns	ns	ns	ns	ns	ns
	dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
broad-leaf	green	ns	ns	ns	**	ns	ns	ns	*	ns
	dead	ns	ns	*	**	ns	ns	ns	**	*
vegetative stem		ns	ns	ns	ns	ns	ns	ns	ns	ns
flower stem		ns	ns	ns	ns	ns	ns	ns	ns	*
seed/flowerhead		ns	ns	ns	ns	ns	ns	ns	ns	ns
Juncus	green	ns	ns	ns	ns	ns	ns	ns	ns	ns
	dead	ns	ns	ns	ns	ns	ns	ns	*	ns
Carex	green	ns	*	ns	*	ns	ns	ns	ns	ns
	dead	ns	*	ns	*	ns	ns	ns	ns	ns
Galium	green	ns	***	ns	**	ns	ns	ns	ns	ns
	dead	ns	ns	ns	ns	ns	ns	ns	ns	ns
other dicot.	green	ns	ns	ns	ns	ns	ns	ns	ns	ns
moss		ns	ns	ns	ns	ns	ns	ns	ns	ns

G = goat; D = red deer; C = guanaco
ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Table 8.4: Summary of statistically significant differences in the contribution of vegetation categories to the diets consumed by goats, red deer and guanacos on the Calluna community.

green *Calluna vulgaris* shoots in the deer and goat diets. Statistically significant differences in the consumption of *Vaccinium myrtillus*, another major component of the sward, were less consistent.

The significantly greater amounts of *Carex* spp. and *Juncus* spp. identified in the guanaco diet are evident but not consistently significantly different.

8.2 DIET DIGESTIBILITY

8.2.1 *In vitro* digestibility

The digestibility coefficients of the diets consumed by the three species of animal on each occasion as estimated from *in vitro* digestibility determinations are depicted in Figure 8.4.

Irrespective of session or season no differences were found in the digestibilities of the diets consumed by the three species of animal when selecting from either the sown or indigenous grassland communities (Table 8.5). Although no significant differences were recorded for the dwarf-shrub community in summer 1991, during spring 1992 the coefficient of digestibility of the diets selected by the guanacos was significantly lower than that of the diets selected by the goats and red deer. However in summer 1992 the digestibility of the guanaco diet was higher than that selected by the goats.

8.2.2. Diet digestibility as determined using n-alkanes

Figure 8.5 compares the digestibility of the diets consumed by the three species of animal on each occasions as determined using the n-alkane technique. A greater number of significant differences were identified among the digestibility coefficients estimated using the n-alkane technique (Table 8.6). However, there was no consistency between sessions or seasons in the differences obtained.

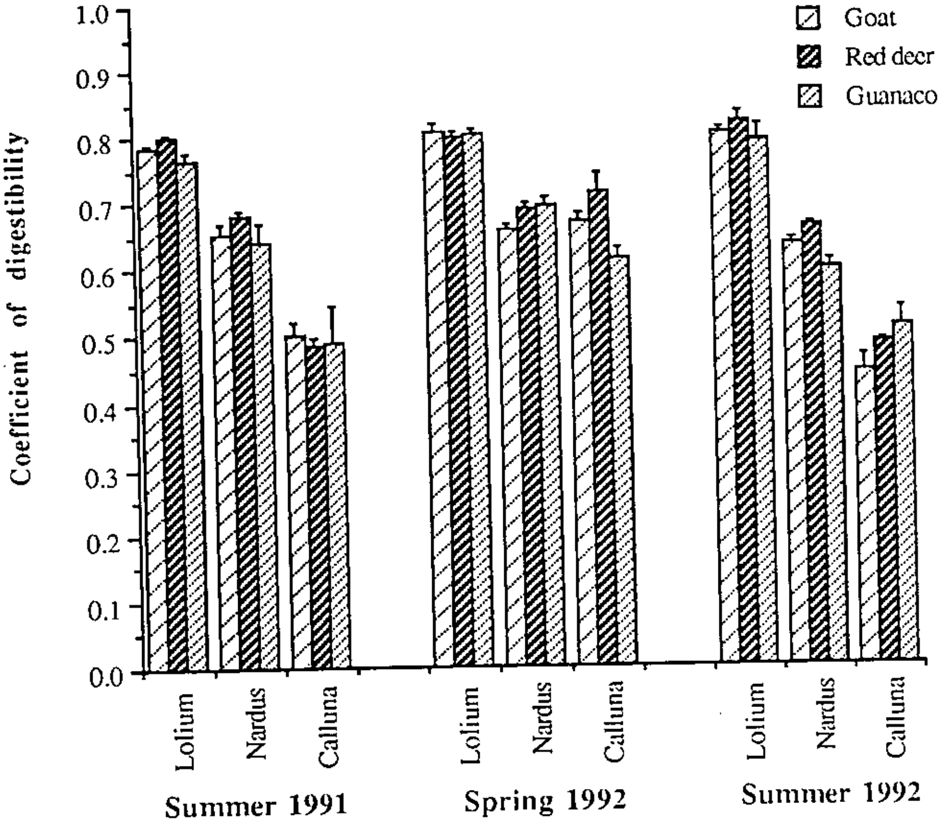


Figure 8.4: Comparison of *in vitro* digestibility of diets consumed by goats, red deer and guanacos.

Session	Vegetation	Goats v. Red deer	Goats v. Camelids	Red deer v. Camelids
Summer 1991	Lolium	ns	ns	ns
	Nardus	ns	ns	ns
	Calluna	ns	ns	ns
Spring 1992	Lolium	ns	ns	ns
	Nardus	ns	ns	ns
	Calluna	ns	**	**
Summer 1992	Lolium	ns	ns	ns
	Nardus	ns	ns	ns
	Calluna	ns	**	ns

ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Table 8.5: Summary of statistical differences between species in diet digestibility, as determined using in vitro analysis.

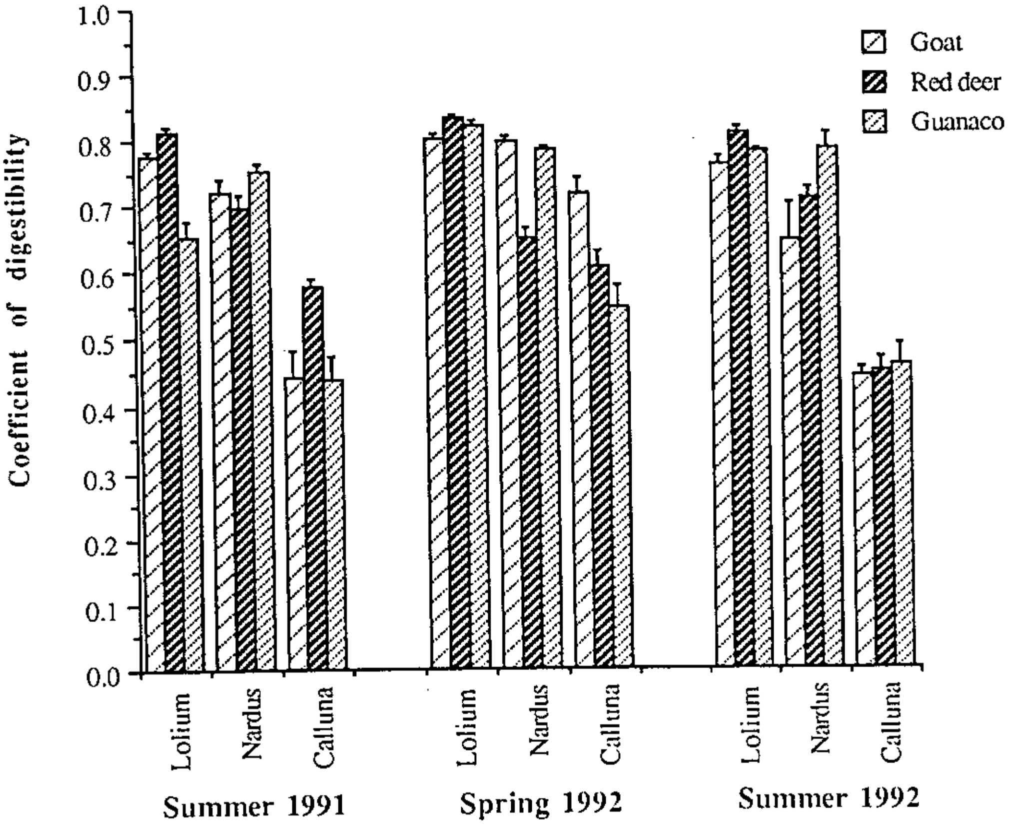


Figure 8.5: Comparison of digestibility of diets consumed by goats, red deer and guanacos as determined using the n-alkane technique.

Session	Vegetation	Goats v. Red deer	Goats v. Camelids	Red deer v. Camelids
Summer 1991	Lolium	ns	**	***
	Nardus	ns	ns	ns
	Calluna	**	ns	**
Spring 1992	Lolium	ns	ns	ns
	Nardus	***	ns	**
	Calluna	**	***	ns
Summer 1992	Lolium	ns	ns	ns
	Nardus	ns	**	ns
	Calluna	ns	ns	ns

ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Table 8.6: Summary of statistical differences between species in diet digestibility, as determined using the n-alkane technique.

The digestibility of the diet consumed by the guanacos in summer 1991 on the Lolium sward was lower than that of the diets of the goats and red deer, yet during both sessions in 1992 there were no differences identified between any of the diets selected. Although no differences were recorded on the indigenous grassland in summer 1991, the digestibility of the diet selected by the red deer from the Nardus community in spring 1992 was significantly lower than that of either the goat or guanaco diet, while in the summer session of the same year the coefficient of digestibility of the guanaco diet was significantly higher than that of the goat diet. The digestibility of the red deer diet was significantly lower than either the goat or guanaco diets on the dwarf-shrub community in summer 1991. In spring 1992 the material consumed by the goats was significantly more digestible than that selected by either red deer or guanacos. However, during the second summer session the digestibility of the diets of all three species were similar.

8.3 INTAKE

8.3.1 Organic matter intake

Intakes were converted from kgOM/day to gOM/kgLW$^{0.75}$ for comparisons between the three species, and these values are depicted in Figure 8.6.

There is no consistent pattern to the statistically significant differences in OMI per unit metabolic weight identified between species (Table 8.7). During summer 1991 the red deer consumed significantly more than the guanacos on the grassland communities, and significantly more than both the goats and guanacos on the Calluna community. In spring 1992 no differences between species were recorded on the sown sward. However, on the indigenous grassland the goats consumed significantly more than both the red deer and guanacos. Their OMI was also significantly higher than that of the guanacos on the dwarf-shrub community. In contrast, during the summer session later the same year intakes of the three species were similar on the indigenous communities, while significant differences were instead recorded on the sown sward; with the red deer

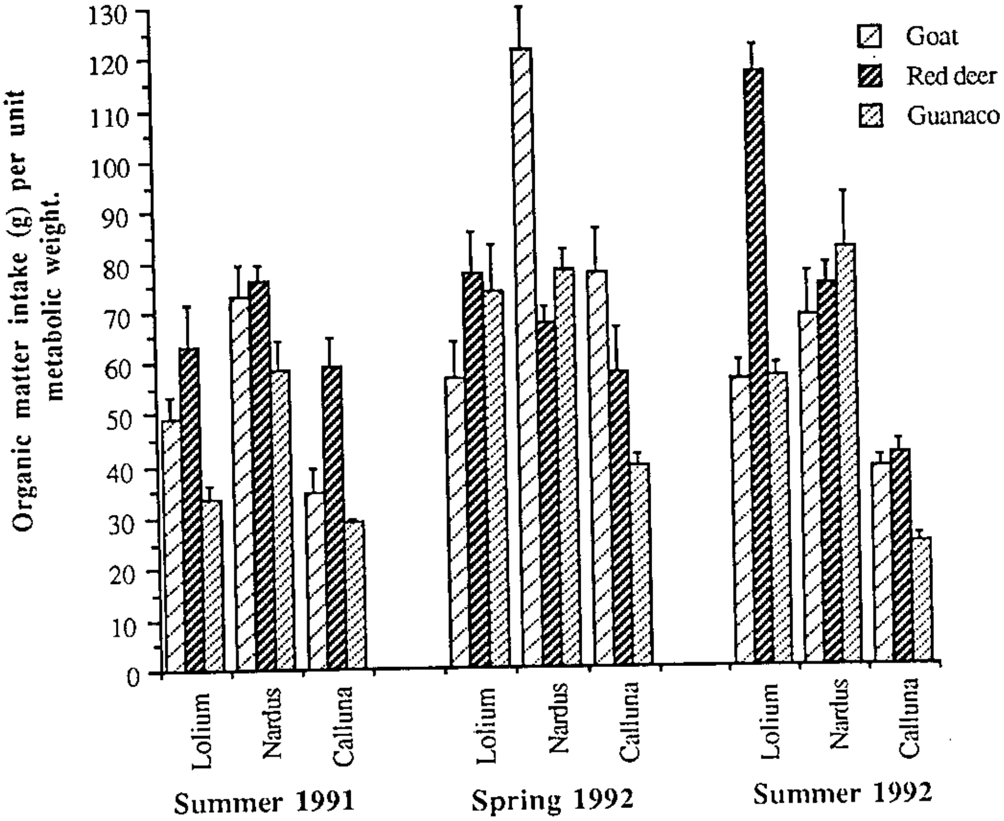


Figure 8.6: Comparison of organic matter intake per unit metabolic weight of goats, red deer and guanacos.

Session	Vegetation	Goats v. Red deer	Goats v. Camelids	Red deer v. Camelids
Summer 1991	Lolium	ns	ns	**
	Nardus	ns	ns	*
	Calluna	*	ns	**
Spring 1992	Lolium	ns	ns	ns
	Nardus	***	**	ns
	Calluna	ns	**	ns
Summer 1992	Lolium	***	ns	***
	Nardus	ns	ns	ns
	Calluna	ns	ns	ns

ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Table 8.7: Summary of statistical differences between species in organic matter intake per unit metabolic weight on different vegetation communities.

consuming more than either the goats or guanacos.

8.3.2 Digestible organic matter intake

Again comparisons were made on a metabolic weight basis, and these are depicted in Figure 8.7.

There was no consistent pattern to between-species comparisons of DOMI (Table 8.8). During summer 1991 the red deer had significantly higher DOMIs than both the goats and guanacos when grazing on the sown sward and dwarf-shrub community. In contrast, during the spring session the DOMI values for the three species on the sown sward were similar, while those of the goats were significantly higher on both indigenous communities. However, during the summer session later the same year DOMI values for the red deer were again significantly higher than those of the goats or guanacos on the sown sward. The only difference recorded on the indigenous vegetation types was a higher DOMI for the guanacos in comparison with the goats on the Nardus community.

8.4 GRAZING PATTERN

8.4.1 Total grazing time

The total grazing times of the three species of animal on each vegetation type on each occasion are plotted in Figure 8.8. Irrespective of season, session or vegetation type the total time spent by the goats grazing each day was significantly less than that of either the red deer or camelids (Table 8.9).

Of the three sessions on the sown pasture, only during summer 1992 was there a significant difference in grazing time between the red deer and camelids; with the total for the latter being significantly higher. On the indigenous grassland, grazing times for these two species were similar on all occasions. In contrast, on the dwarf-shrub community the red deer grazed significantly longer each day than the camelids during

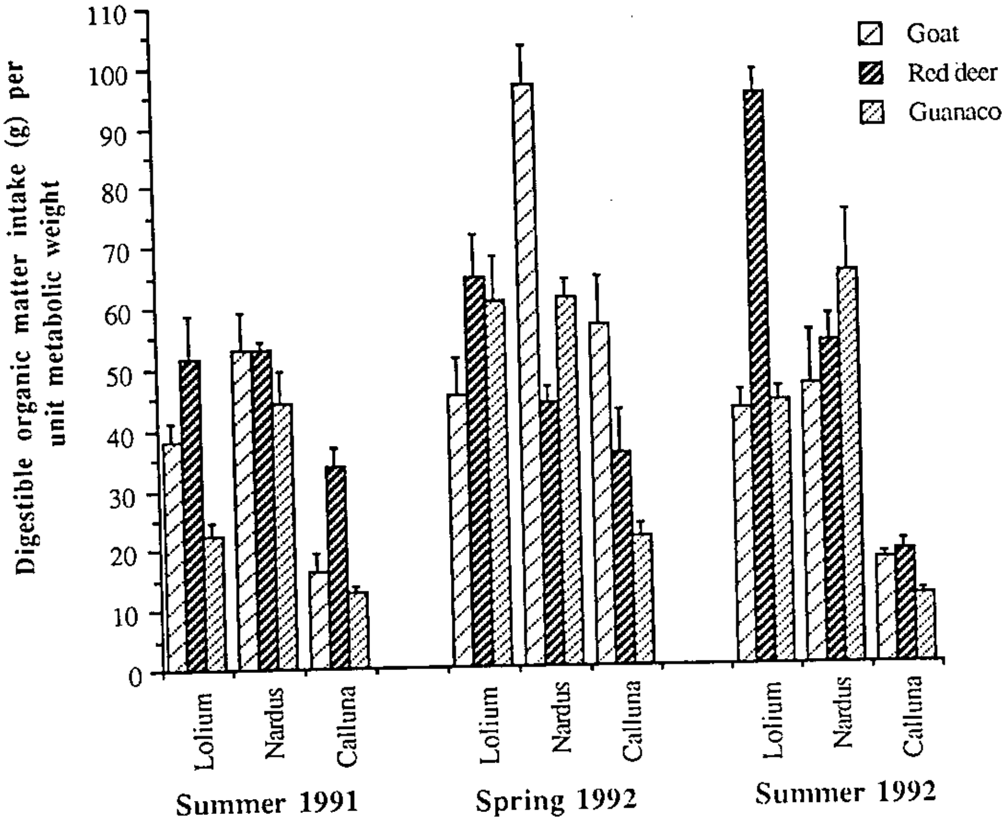


Figure 8.7: Comparison of digestible organic matter intake per unit metabolic weight of goats, red deer and guanacos.

Session	Vegetation	Goats v. Red deer	Goats v. Camelids	Red deer v. Camelids
Summer 1991	Lolium	*	*	***
	Nardus	ns	ns	ns
	Calluna	*	ns	**
Spring 1992	Lolium	ns	ns	ns
	Nardus	***	**	ns
	Calluna	*	**	ns
Summer 1992	Lolium	***	ns	***
	Nardus	ns	*	ns
	Calluna	ns	ns	ns

ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Table 8.8: Summary of statistical differences between species in digestible organic matter intake per unit metabolic weight on different vegetation communities.

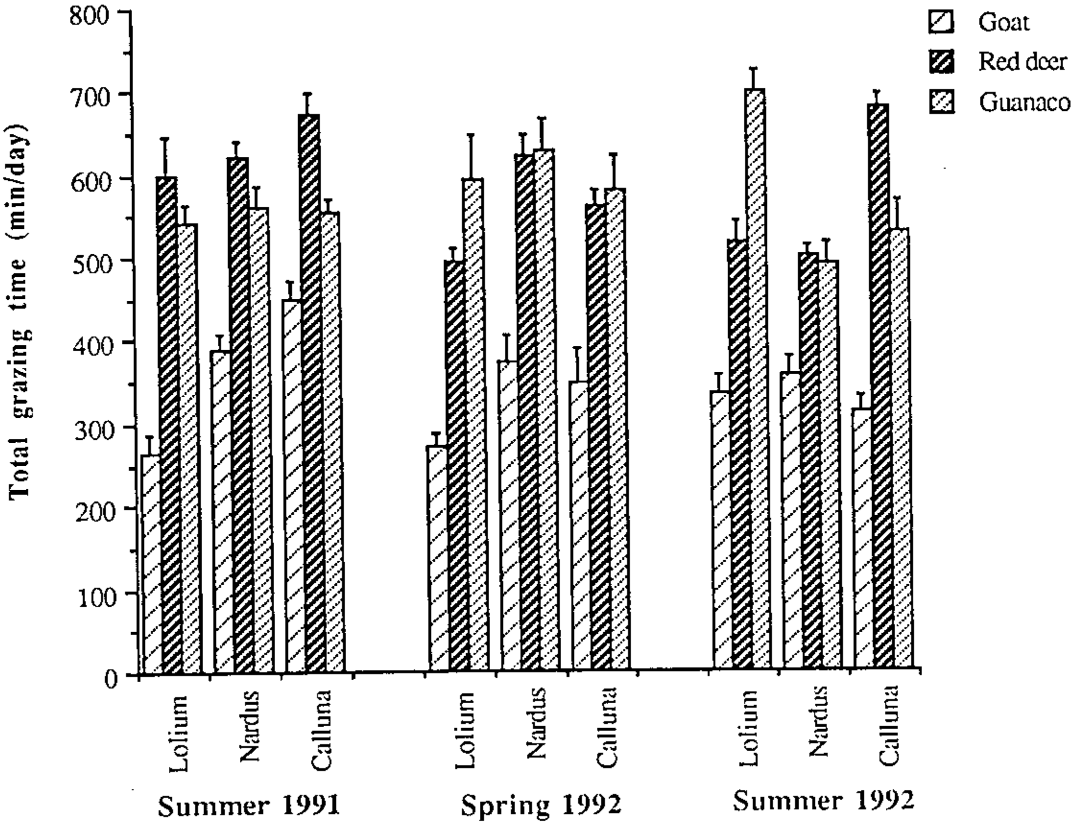


Figure 8.8: Comparison of total grazing time of goats, red deer and guanacos.

Session	Vegetation	Goats v. Red deer	Goats v. Camelids	Red deer v. Camelids
Summer 1991	Lolium	***	***	ns
	Nardus	***	***	ns
	Calluna	***	*	*
Spring 1992	Lolium	***	***	ns
	Nardus	***	***	ns
	Calluna	***	***	ns
Summer 1992	Lolium	***	***	***
	Nardus	***	***	ns
	Calluna	***	***	**

ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Table 8.9: Summary of statistical differences between species in total grazing time on different vegetation communities.

both summer sessions.

8.4.2 Bite rates

The bite rates recorded for each species on each vegetation type are plotted in Figure 8.9.

During summer 1991 and spring 1992 the bite rates of the three species of animal were similar, irrespective of vegetation type (Table 8.10). Likewise, no significant differences were identified between the bite rates of the three species on either the Nardus or Calluna communities in summer 1992, However, on the sown sward the bite rate of the camelids was significantly higher than that of either the goats or red deer.

8.5 DISCUSSION

The number of plot effects and plot x session interactions identified when statistically analysing the results for the composition of the goats' diet (Chapter Five) indicate that this species exhibited greater variability both between and within individual animals in the diets selected than either the red deer (Chapter Six) or South American camelids (Chapter Seven). By repeated sampling of the environment an animal accumulates information regarding the spatial and temporal variance in food availability (Stephens, 1987). This will be of more benefit to animals of small body size, such as goats, which are unable to compensate for consumption of diets of lower nutritional value by increasing transit time (Demment and Greenwood, 1988) and must instead rely on selection of high quality items from the range available. In a heterogeneous environment this will lead to frequent changes in diet composition to exploit variations in digestibility of plant species at different stages of maturity or the appearance of ephemeral plant species.

The relatively homogeneous sown sward offered comparatively little opportunity for

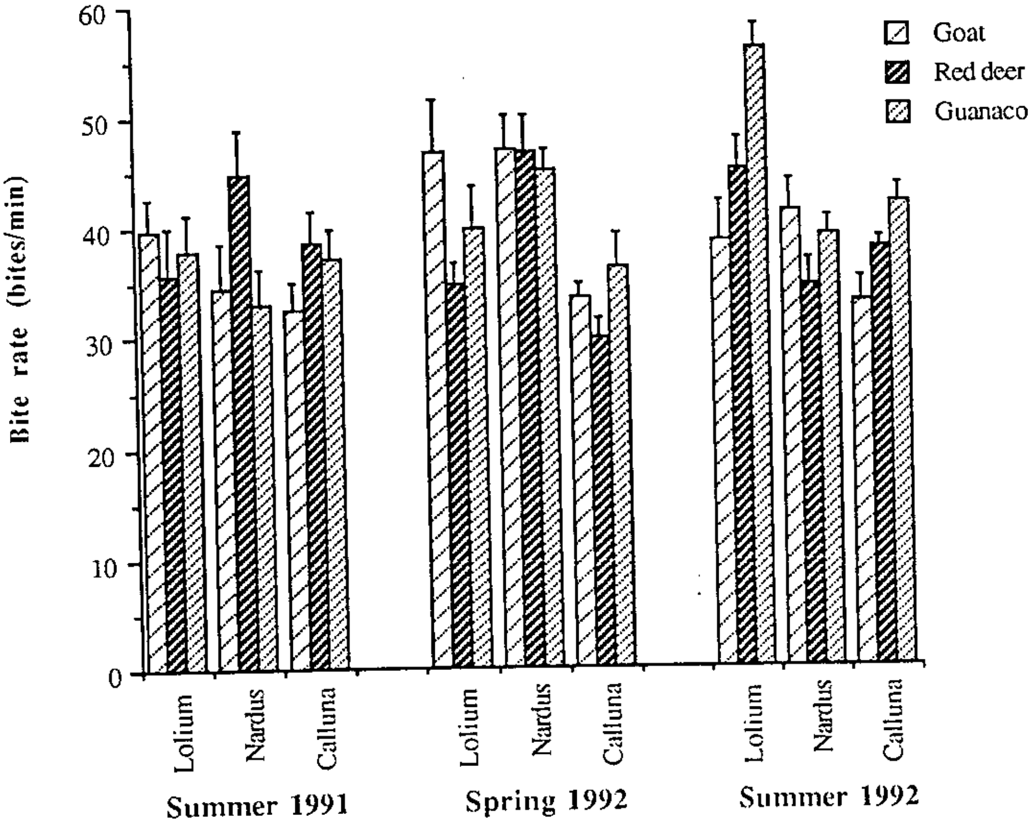


Figure 8.9: Comparison of bite rates of goats, red deer and guanacos.

Session	Vegetation	Goats v. Red deer	Goats v. Camelids	Red deer v. Camelids
Summer 1991	Lolium	ns	ns	ns
	Nardus	ns	ns	ns
	Calluna	ns	ns	ns
Spring 1992	Lolium	ns	ns	ns
	Nardus	ns	ns	ns
	Calluna	ns	ns	ns
Summer 1992	Lolium	ns	***	**
	Nardus	ns	ns	ns
	Calluna	ns	ns	ns

ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$

Table 8.10: Summary of statistical differences between species in bite rates on different vegetation communities.

selective grazing yet all three species of animal consumed material from the various vegetation categories in different proportions to those present in the sward. Although green grass lamina was the main dietary component for all three species on each occasion, inter-specific differences in the contribution of minor sward components, including *Trifolium repens*, to each diet were identified. These differences suggest niche separation (Gordon and Illius, 1989) between the species which could potentially be exploited to increase the productivity of grazing systems, even on sown swards.

Previous work has found evidence of an increase in clover content of pasture grazed by goats (Radcliffe and Francis, 1988), and associated gains for sheep (McGregor, 1985; Radcliffe, Townsend and Baird, 1991). As clover consumption during the current study was similar for goats and red deer, the implication is that red deer too could have a beneficial role in management of sown swards for sheep production. However, the most dramatic effect could be achieved by prior grazing by camelids. Whereas the goats and red deer were found to have selected green clover leaf, the camelids consistently avoided this vegetation category. Accounting for this difference between the species in their response to clover is difficult. Factors previously identified as influencing the consumption of this plant, such as its vertical distribution within the sward (Milne *et al*, 1982) or the clover content of the sward previously grazed (Newman, Parsons and harvey, 1992) can be disregarded in this context. The quantities of grass vegetative stem and flowerstem in the camelid diets indicate that like the goats and red deer they were consuming material from all strata of the sward; and all three species had grazed together during the 'run-in' period. Instead the avoidance of clover leaf and other dicotyledonous plant species (Chapter Seven) may be a response to the secondary chemicals that are employed by plants as defences against herbivory and appear to be better developed in dicotyledons than in graminoids (Malechek, Balph and Provenza, 1986). As yet there has been no comparison with conventional ruminants of the susceptibility of South American camelids to plant secondary compounds. In light of the results of this study this is an important topic for further research.

Camelid grazing could also have a beneficial effect on the grass species within a grass/legume sward as the increased consumption of dead lamina and flowerstem will encourage tillering and vegetative growth (Penning *et al.*, 1991). In contrast persistent avoidance of dicotyledonous plants perceived as weeds has been noted as resulting in what would generally be regarded as a detrimental increase in the levels of such species in the sward (M.D. Fraser, pers. obs.).

While the correlation coefficients between the goat and red deer diets were highest on the sown sward, on the indigenous grassland the diets of the red deer and guanacos were most similar. Indeed during the spring experimental session no significant differences in the proportions of the respective diets accounted for by any of the twenty-six vegetation categories were identified.

Considering the quantity of inter-tussock herbage on offer and the preferences of cattle and sheep on similar vegetation (Grant *et al.*, 1985; Grant and Hodgson, 1986), avoidance of the *Nardus stricta* tussocks by all three species of animal was predictable. The palatability of this species would be lowest during the summer sessions when characteristic bristle-like hairs are present on mature leaves, and during these experimental periods the goats were more fastidious in their avoidance of this species than either the red deer or camelids. This, together with the goats relatively lower consumption of dead lamina of the main dietary component, broad-leaved grasses, suggests that they were more adept at selecting desired plant species and/or plant parts from the array available then the other two species. This ability of the goats to demonstrate a greater degree of discrimination will also have contributed to the increased variability in dietary composition of this species noted previously, particularly on the heterogeneous communities. The goats could be anticipated as exhibiting more selectivity than the red deer, since red deer have comparatively broad mouths more akin to cattle. In comparison, on the evidence of mouth characteristics alone the camelids would be expected to be equally discriminating as goats. Both goats and guanacos have relatively narrow incisor arcades allowing discrete food items to be prehended and ingested (Grant *et al.*, 1985; Illius and Gordon, 1987; Gordon and Illius 1988). Instead it would appear that by virtue of their greater body size the camelids like the red deer could afford to be more tolerant than the goats of poorer quality items (Illius and Gordon, 1991). However, the difference in selectivity between the goats and the two larger species was not reflected in the estimates of diet digestibility, presumably as a result of the relative abundance of preferred sward components such as green lamina of graminoid species. In situations where the animals are restricted by overall herbage biomass in general, and the availability of preferred sward components in particular, the differences in selectivity are more likely to translate to differences in diet digestibility.

On the indigenous grassland community a significantly higher proportion of flowerstem and seed/flowerhead was recorded in a diet selected by the camelids. Previously higher proportions of seedhead have been identified as a characteristic of goat diets and complementary grazing with cattle and sheep investigated (Russel, 1989). However, although the diets of sheep and cattle contained more green leaf and less seedhead when grazed with goats than when grazed on their own the effects were not sufficiently large or consistent to be reflected in increases in animal production. As yet no similar studies implementing sequential rather than complementary grazing systems have been carried out, yet the potential of goats or camelids to improve under-grazed swards for cattle or sheep is worthy of assessment. Certainly sward conditions, such as tall stemmy plants, high density of inflorescences, and presence of senescent material have been found to prevent cows from taking large bites with the result that forage intake was reduced (Stobbs, 1973).

In contrast, without careful management red deer may have an opposite effect on pasture. This species has been reported as grazing less intensively than domestic stock (Kay and Staines, 1981). This could reduce the possibility of destructive overgrazing, but with respect to the annual vegetation cycle may allow earlier maturation of the grasses and consequently lower sward digestibility.

There were no differences similar to those identified on the sown sward in the consumption of dicotyledonous plants by the camelids in comparison with either the goats or red deer were not evident on the Nardus sward. However, the contribution of dicotyledonous plants to the Nardus community was so small that, although the goats and red deer consumed this category in similar proportions to that available in the sward, the amounts in the diets were negligible.

In general the same plant species were selected by all three species of animal from the Calluna community, and these correspond to those previously recorded as preferred by cattle and sheep (Grant *et al.*, 1987). While the sward stack-graphs indicate that the composition of the Calluna community was consistent between sessions, there were indications of a seasonal change in the composition of the diets selected by all three species, with in general grasses and *Vaccinium* spp accounting for a greater proportion of the material consumed in spring. This is in keeping with other studies of domestic and semi-domestic herbivores on Callunetum which have identified a seasonal shift in utilisation of heather in response to changes in grass quality. Both goats (Bullock, 1985) and red deer (Colquhoun, 1971) have been shown to exhibit similar seasonal variations in diet to those reported for hill sheep (Grant *et al.*, 1976) with grasses and sedges the main dietary components in summer and increased use of ericaceous shrubs occurring in winter. Further studies investigating grazing behaviour of sheep on heather and associated areas of sown grass or Agrostis/Festuca have shown that amount of grass (height (cm) and weight (kg DM/ha)) is a major determinant of the utilisation of heather

(Grant and Hodgson, 1986).

Irrespective of season, consumption of the flowers of *Calluna vulgaris* was similar for all three species. During the spring experimental session the contribution of other morphological units of *Calluna vulgaris* to the diets of each species of animal was also comparatively similar with only a difference between the levels of green shoots in the red deer and goat diets identified. In contrast during the summer sessions ,when heather is growing and most nutritious, the red deer diet contained significantly more *Calluna vulgaris* shoots, both live and dead, than either the goat or camelid diet; and also more wood than the goat diet. Thus not only was *Calluna vulgaris* making a greater contribution to the red deer diet *per se*, they were utilising more of the plant and grazing deeper into the heather canopy, although in general still avoiding this plant relative to its contribution to the sward profile. This agrees with observations that red deer took more of the whole heather plant than sheep (Hobson *et al*, 1976) and corresponds to results for cattle on similar vegetation (Grant *et al.*, 1987). Thus deer like cattle would be expected to have a greater impact on individual *Calluna vulgaris* plants than sheep, goats or camelids. This increased utilisation of heather will help maintain the stand in a more juvenile condition (Grant *et al.*, 1978), and could be used to prolong the useful period after burning, and increase the time interval between burnings. However, by removing more of the shoot length they increase the risk of shoot death and the incidence of broken or uprooted shoots.

While the response of the goats and guanacos to the Calluna community was similar during the current study, differences in selectivity exhibited by these two species implies their responses to this type of dwarf-shrub community would be different were the availability of the preferred graminoid species to be reduced. The catholic nature of the goats' feeding habits during this study, together with results from previous work on this type of vegetation community (Bullock, 1985; Gordon, 1989b; Gordon, 1989c) indicates that this species would be willing to increase its consumption of *Calluna vulgaris*. In contrast, the general avoidance by the guanacos of dicotyledonous plants, and their relatively high consumption of dead material, suggest that they would consume a diet of even lower digestibility and/or reduce their intake further to avoid eating *Calluna vulgaris*.

Selective behaviour (Squibb, Provenza and Balph, 1990) and forage intake (Hodgson and Jamieson, 1981) have been shown to be influenced by previous exposure to a diet. While the red deer had spent a large portion of their life prior to this study on Callunetum, neither the goats nor camelids had grazed this type of sward before. Although as much time as possible was allocated for adjustment to each vegetation community, differences in selectivity depending on previous experience of a particular pasture have been identified among sheep (Arnold *et al.*, 1964) and steers (Carulla, Lascano and Ward, 1991) which suggest an adaption period of several weeks or even months may be required.

For all three species of animal estimates of diet digestibility derived from *in vitro* determinations were consistently higher on the Lolium sward than on either of the indigenous communities. This agrees with previous work studying cattle and sheep on similar pastures (Hodgson *et al.*, 1991), who concluded that variations in the digestibility of ingested herbage were reflected in variations in herbage intake within and between the grassy communities. An exception was lower intakes on the ryegrass sward than on the hill grass community despite the generally higher digestibility of herbage eaten from the ryegrass sward. These results were repeated by the goats and camelids during the present study on similar vegetation communities. Accounting for these differences is not straightforward (Chapters Five and Seven). One factor involved may have been the length of the ryegrass pasture. The height of the Lolium sward during the current study ranged from 9.5cm to 20cm, and Penning *et al.* (1991) found evidence that tall swards, i.e. those greater than 9cm, deteriorated in structure. Similarly, it has been suggested that when plant availability is not limiting intake rate will be a function of the rate at which the herbivore can process and swallow food (Spalinger, Hanley and Robbins, 1988) and as a sward becomes taller more jaw movements are associated with chewing (Laca *et al.*, 1992).

During both summer sessions the diets selected by all three species from the indigenous grassland were significantly more digestible than those consumed on the dwarf-shrub community; again in keeping with results for cattle and sheep (Hodgson *et al.*, 1991). However, for the goats and red deer digestibilities of the diets selected from these two vegetation types were similar during the spring experimental session. In each case this was related to a significant increase in the digestibility of the diet on the Calluna sward in spring relative to either summer session on the same community.

When the oesophageal fistulated animals were selecting from the sown and indigenous grasslands, the digestibility of the diets consumed by the three species of animal was similar irrespective of season or session. In contrast, differences were identified on the dwarf-shrub community, although these highlight variability in the camelid diet relative to the other two species rather than a consistent trend. Due to the relative rarity of the *Juncus* spp. and *Carex* spp. being selected by the camelids the composition and digestibility of extrusa samples collected by these animals over the comparatively short sampling period varied. This is reflected in the greater standard errors for the digestibility of the diets selected from the dwarf-shrub community by these animals and will have contributed to the between-species differences identified.

The results of the statistical analysis of the *in vitro* digestibility determinations do not correspond to differences in digestibility identified using the n-alkane method. These disparities cannot be attributed to a particular session or community. For example, using the n-alkane technique differences were found during the summer 1991 session on the sown sward and both sessions in 1992 on the indigenous grassland. Likewise significant differences identified during the summer session on the Calluna community conflict with those obtained from *in vitro* analysis. Given the circumstances under which the data was collected it is only possible to speculate on the reasons for these differences but a number of potential sources of bias can be identified. For example, rumen liquor donors of the same species as the study animals were not available and consequently sheep inoculum was used. These were maintained on a diet which was different (good quality hay) to the plant material being assessed and this could also have influenced the digestibility estimates derived (Huston *et al.*, 1986), particularly in the case of samples containing browse (Nastis and Malechek, 1988). Likewise, the Tilley and Terry (1963) *in vitro* procedure does not take into account variations in rumen retention time between different forages consumed by the same species or among animal species. Clearly conventional digestibility trials are urgently required to compare the *in vitro* and n-alkane methods of estimating diet digestibility with *in vivo* digestibility for a range of forages.

Since the n-alkane results were derived from the intact core grazing animals comparisons involve results from different animals. Thus differences in diet composition could be responsible for differences in diet digestibility. However, comparison of the odd long-chain alkanes C_{29} to C_{35} in the faeces samples of the grazers and oesophageal fistulated animals of each species revealed no consistent differences suggesting the long-term diets consumed were broadly similar. This concurs with observations which suggest diets selected by fistulated and non-fistulated animals are similar (Forbes and Beattie, 1987). Likewise comparisons of the alkane profiles of faeces samples collected from the oesophageal fistulated animals and the extrusa samples indicated that with the exception of the material collected by the camelids during sampling sessions on the Calluna community (see Chapter Seven) the composition of extrusa samples was likely to be representative of the long-term diet. However, such comparisons rely on components within the sward having sufficiently individual alkane profiles to ensure that if the proportions of a plant species and/or plant part significantly different between samples then this is reflected in the overall alkane profile changing. While *Trifolium* spp. (Dove, 1992) and *Calluna vulgaris* (R.W. Mayes, pers. com.) have been shown to have characteristically different profiles from graminoids, discrimination between grass species or morphological units of a given plant is more difficult (R.W. Mayes, pers. com).

Examination of oesophageal extrusa has been identified as the most accurate of the methods currently available for determining the diets of free-roaming herbivores (McInnis, Vavra and Krueger, 1983). However, extrusa samples only reflect the animals' response to the limited amount of experimental vegetation they encounter during a particular collection period. When fistulated animals are selecting from a heterogeneous, structurally complex sward the likelihood of this vegetation and the associated foraging opportunities being similar for each animal or for a given animal of different occasions is minimal, even if the animals have been given adequate opportunity to become familiar with the measurement area. The only way of overcoming this problem would be to collect samples over a longer period of time. However, with the conventional system of fistula creation and maintenance (Cook *et al.*, 1963) prolonged plug removal is not feasible. In an attempt to overcome these limitations the possibility of incorporating a radio-controlled valve has been recently investigated (Raats and Clarke, 1992). Such a system could lead to extrusa samples being made up of boluses collected at regular intervals during the course of a whole day rather consisting of all the material consumed during one thirty minute grazing bout. It would also be advantageous if animals which are reluctant to sample, such as camelids, are being studied.

During grazing trials on similar vegetation types it was found that sheep tend to maintain diet digestibility at the expense of rate of intake, whereas cattle tended to maintain rate of intake at the expense of digestibility (Armstrong and Hodgson, 1986). In the case of the current research project there was no obvious relationship between the differences in diet digestibility between species identified by either method and the differences in intake between the three species Estimates of herbage intake for grazing animals are highly variable, but those considered most valid in the review of Cordova, Wallace and Pieper (1978) show a range from 1% to 2.8% of body weight per day. This compares with 1.3% to 4.6% for the goats; 1.3% to 2.4% for the red deer (excluding Lolium summer 1992 - Chapter Six); and 0.8% to 2.5% for the camelids.

Sudies reviewed by Louca, Antoniou and Hatzipanayioutou (1982) and more recent work by Domingue, Dellow and Barry (1991b) conclude that, although dry matter intake (g/kgLW$^{0.75}$) for goats tends to be higher than for sheep it is always lower than for cattle. Since intakes of red deer have been found to be significantly higher than those of sheep irrespective of season (Milne *et al.*, 1978) higher intakes for the red deer relative to the goats during the current study are feasible. In contrast, lower intakes on a metabolic weight basis have been reported for South American camelids in comparison with sheep (San Martin and Bryant, 1989) suggesting intakes for both the goats and red deer could be expected to be higher than those for the guanacos. Consequently differences between the intakes of the red deer and guanacos could be anticipated. Although a number of significant differences were identified between species these were not consistent and there was there no clear pattern to interactions with vegetation type or season. Indeed, since the summer 1991 results for the camelids must be treated with caution as a result of the reliance on extrusa samples from only one oesophageal fistulate, the only highly significant differences are associated with an extraordinarily high intake figure for one of the species (goats on Nardus in spring 1992 and red deer on Lolium in summer 1992) it would appear to be more appropriate to stress the similarity of the results. This similarity seems largely due to the camelid intakes being higher than those previously recorded (Farfan *et al.*, 1986; San Martin and Bryant, 1989). The high organic matter intakes of the goats on the Nardus community in spring 1992 and red deer on the Lolium sward in summer 1992 have also clearly influenced the between-species differences in DOMI recorded on these occasions.

Irrespective of vegetation type or session, the total time spent grazing by the goats was significantly less than that of the red deer or guanacos. In contrast, differences in grazing time between cattle and sheep on similar vegetation types to those grazed during this study were not significant (Hodgson *et al*, 1991). While the times spent grazing per day by the red deer and guanacos are similar to those recorded for the cattle and sheep, the grazing times for the goats are substantially lower. That grazing times for each of the three species were relatively insensitive to vegetation type during the current study agrees with equivalent findings for cattle and sheep (Hodgson *et al*, 1991).

The kappa coefficients which were calculated (Chapters Five, Six and Seven) indicate that all three species of animal exhibited synchronised grazing activity. Although this synchronisation is associated with reduced predation, the resulting competition for availability of forage among members of a group could reduce the opportunity for selective feeding. Vegetation type did not have a consistent effect on the synchronisation of any of the three species of animal. Of the three species studied the camelids had the highest kappa coefficients for grazing and total activity. These were generated from distinctive vibracorder traces (Chapter Seven) which implied the animals had grazed almost continuously during daylight hours. Had the coefficients been calculated from jaw-recorder data summarised on a minute by minute basis the results may have been markedly different. The kappa coefficients of grazing and total activity for the goats are lower than those for the guanacos and broadly similar to values generated for sheep (Rook and Penning, 1991). The lowest coefficients recorded were for the red deer and these will have been influenced by their grazing during both day and night.

With the exception of the higher bite rate of the camelids on Lolium in summer 1992, no significant differences were recorded between the bite rates of the three species. In contrast within-species differences were identified. In the case of the goats and guanacos these would be expected to account for the differences in intake on different vegetation types since grazing time was generally similar on each occasion. For example, the selection by the guanacos of the highly clumped *Juncus* spp. (Chapter Four) on the Calluna community would be expected to correspond to an increase in search time and decrease in bite rate. That such differences were not recorded may be largely due to observational error during data collection. Particularly on the indigenous communities the mouthparts of the grazing animals were obscured by the abundant vegetation. The topography of the experimental areas also hindered visibility. As a result records were made of head jerks which were presumed to accompany bites but which may have been associated with manipulative jaw movements during selective feeding. If jaw recorders (Penning, 1983; Penning, Steel and Johnson, 1984) could be adapted to cope with the treatment they would receive from semi-domesticated animals insensitive to equipment fragility a more detailed interpretation of the entire grazing process would be possible. Only then will it be clear whether the perceived differences in vegetation breakdown during chewing were related to between-species differences in chewing or rumination patterns.

When the potential sources of error in the bite rate results were considered, it became apparent that it was inappropriate to use this data to derive additional information such as bite mass. Considering the array of studies which include this type of information, it would appear that a valuable opportunity for comparisons with data which has influenced the current understanding of the foraging strategy of herbivores has therefore been missed. However, the limited applicability of results generated during short-term studies would have had to be taken into account. Thus, even if accurate estimates of bite mass could be calculated for the goats, red deer and guanacos, opportunities for comparisons with equivalent data for other free-roaming animal species would have been limited.

Despite the acknowledged problems of extrapolating data collected from short-term studies, as yet there has been no attempt to apply the approaches and techniques developed to more realistic conditions. While the use of artificial swards has provided an illuminating perspective on the underlying mechanistic processes involved in plant/animal interactions (Laca, Ungar and Demment, 1994; Parson *et al.*, 1994), more data from detailed studies is now required to counteract the increasingly reductionist approach of recent times. With recent developments in data-recording equipment incorporating advances in electronic and computer technology (Roberts, Williams and Last, 1993) to produce comparatively light-weight devices which would require little modification for use on long-term studies on free-roaming animals, the opportunities for detailed research on truly heterogeneous vegetation are multiplying.

Even within the context of the current project numerous avenues for further research can be identified. As the current study was a baseline experiment an obvious approach for follow-up work would be to investigate how each species alters its diet composition and/or ingestive behaviour to accommodate reductions in the availability of preferred plant species and plant parts. In particular, more information is required on the effects of reducing inter-tussock herbage availability and graminoid availability on the consumption of *Nardus stricta* and *Calluna vulgaris* respectively. Without this information it is impossible to accurately predict how each animal species will respond to the changes in vegetation composition and canopy structure brought about by prolonged grazing, or, conversely, the long-term effects of grazing on the vegetation community. Alternatively biomass and overall composition could be kept constant and combinations of different horizontal and vertical distributions of sward components used to investigate the trade-off between maintaining intake and selective feeding.

Another area requiring clarification is how the grazing ecology of these species would be affected by co-species grazing. Thus, while a variety of differences in diet composition which could be exploited in sequential grazing systems have been identified, the question of complementary grazing systems must also be addressed, since resource managers are likely to be interested in mixed species grazing, especially on indigenous communities. In particular, information will be required on if, and how, these animals modify their diet composition and ingestive behaviour when grazing alongside traditional livestock species.

8.6 SUMMARY

1. All three animal species studies are selective feeders. In comparison with the red deer and guanacos, the composition of the goats' diet was very variable, indicating a flexible feeding habit. In contrast, a feature of the diet composition of the red deer was consistency.

2. Guanacos are principally grazers, whereas goats and red deer are intermediate feeders, consuming browse as well as grass.

3. All three species exhibited greater selectivity when grazing on the indigenous communities than when grazing on the sown sward. However, even on the comparatively homogeneous Lolium sward there were significant between-species differences in diet composition. These were primarily related to the guanacos avoidance of clover and other dicotyledonous plants encountered within the sward. In contrast, the goats and red deer consumed green leaf from all plant categories found at or near the sward surface.

4. On the Nardus grassland all three species avoided the dominant tussock-grass and instead selected from the species-rich inter-tussock areas. This resulted in green lamina of broad-leaved grasses being the main dietary component for all three animal species irrespective of season. Between-species differences in minor components worthy of note included an increased contribution of non-grass monocotyledonous plants to the goat diet in spring, and a higher proportion of the camelid diet being accounted for by grass flowerstem and grass seed/flowerhead in summer.

5. The response of the three species of animal to the dwarf-shrub community was also broadly similar. In general all had avoided *Calluna vulgaris* and strongly selected

graminoid species. Consumption of this latter plant group was greatest in spring, then deceased slightly in summer when grass digestibility is reduced and *Calluna vulgaris* is at its most digestible. Although the contribution of flowers of *Calluna vulgaris* to the diets of the three animal species was similar, examples of increased consumption of green shoots, dead shoots and wood of *Calluna vulgaris* by the red deer were identified.

6. The differences in selectivity identified could be potentially exploited to manipulate the species composition and/or canopy structure of the vegetation resource being grazed.

7. In general diet digestibility was higher on the sown sward than on the indigenous communities, and higher on the indigenous grassland than on the dwarf-shrub community. Despite the differences in selectivity identified there were no consistent patterns to between-species differences for digestibility coefficients estimated by either the *in vitro* method or n-alkane technique.

8. When expressed on a metabolic weight basis there was no consistent pattern to the statistically significant differences in OMI identified between species. Both differences in OMI and diet digestibility contributed to between-species differences in DOMI identified.

9. While the goats and guanacos confined their grazing mainly to daylight hours, the red deer grazed during both day and night. Irrespective of season, session or vegetation type the total time spent by the goats grazing each day was significantly lower than that of either the red deer or guanacos. However, bite rates for the three species were generally similar.

10. This study has succeeded in generating data which will provide a scientific basis for the uptake of goats, red deer and South American camelids, and demonstrated that careful consideration must be given to the possibility of using novel species for the implementation of management regimes on a range of vegetation communities of agricultural or conservation importance in the UK. In addition this project has pinpointed areas should be given priority when considering further research with these species.

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