Foraging behaviour of sheep (*Ovis aries* L.)
grazing on swards of
perennial ryegrass (*Lolium perenne* L.)

by

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Thesis submitted for the degree of Doctor of Philosophy,
University of Oxford, Trinity Term 1988.

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ABSTRACT

Foraging behaviour of sheep (*Ovis aries* L.) grazing on swards of perennial ryegrass (*Lolium perenne* L.)
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The grazing behaviour and diet selection of a vertebrate herbivore, the domestic sheep (*Ovis aries* L.), feeding in patchy perennial ryegrass (*Lolium perenne* L.) monocultures was investigated. Heterogeneity or patchiness was created by manipulating (1) the nutritional content of ryegrass, (2) parameters of sward structure e.g. sward height, pseudostem and lamina length, and tiller density, and (3) brightness of ryegrass relative to the background sward. Patches were either fertilised turves transplanted into paddock swards or were created *in situ* by local fertilisation, trimming etc. The background sward was low in nitrogen (<1.0% N dry weight) compared with average ryegrass leys found on farms in British lowland areas.

Sheep preferred to graze in transplanted patches of ryegrass. These patches were structurally similar to the background sward, but were higher in nitrogen content and digestibility as a result of fertilisation. Thus, sheep actively selected more nutritious ryegrass.

There was a significant quantitative relationship between brightness and the nitrogen and water soluble carbohydrate content of ryegrass. Darker green ryegrass had a higher nitrogen content and lower water soluble carbohydrate content than lighter green ryegrass. It is suggested that sheep learned to use brightness as a cue in intra-specific forage selection. They had a high preference for short, dark green patches of similar height to the lighter green, background sward. Sheep also preferred to graze in tall patches of ryegrass (>10 cm taller than the background sward) regardless of their nutritional content or brightness relative to the background sward. It is likely that sheep use a multiplicity of physical cues associated with perennial ryegrass in diet selection. The interaction between structural sward parameters and nutritional content of forage in influencing diet selection requires further investigation.

In further experiments, an optimal foraging model, the marginal value theorem was used to make predictions about the behaviour of sheep grazing in monocultures containing highly preferred transplanted patches of tall, fertilised ryegrass. By manipulating the cost of travel between these good ryegrass patches and by detailed measurements of intake within patches by individual sheep, I was able to make quantitative predictions about the time spent grazing in each patch. Travel time and costs were increased by moving good patches further apart and by hobbling sheep to slow down their speed of movement. As predicted by the marginal value theorem, average time spent in a patch was positively correlated with average travel time between patches. For two sheep, the predicted and observed times spent in patches were statistically similar at low travel times, while at higher travel times, observed times were greater than predicted. For a third sheep, all observed times were greater than predicted. Thus overall, there was not a good quantitative fit between the model and the observed behaviour. While incorporation of the difference in the energetic cost of travel relative to that of grazing in a good patch into the model resulted in an increase in predicted optimal patch residence times, the fit between predicted and observed values was not significantly improved. Reasons for this difference between observed and predicted patch residence times are discussed. However, these experiments demonstrated that patch-use foraging models may be more useful than prey models in investigating grazing behaviour of vertebrate herbivores, and that travel time between patches of forage is a previously unidentified constraint of sheep grazing behaviour.

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Chapter 1

General Introduction

The basis of diet selection in non-insect herbivores has been widely discussed, ever since biologists observed that herbivores exhibit preferences for particular plant species or parts of plants (Milton 1933; C. Linnaeus 1748 cited in Tribe 1950b; Plice 1951; Cowlishaw & Alder 1960; Arnold & Dudzinski 1978; Lambert 1982; Crawley 1983). Herbivores are said to feed selectively and diet preferences to occur when the proportion of a particular item in the diet is greater than its proportion in the herbivore's environment (Crawley 1983; Begon *et al.* 1986). However, as both Crawley (1983) and Begon *et al.* (1986) pointed out, there are a variety of problems associated with demonstrating selectivity in field studies, as will become evident in the following discussion,

1.1 The basis of diet selection in herbivores

Two main hypotheses have been proposed to explain diet preferences of herbivores. It has been suggested that diet selection may be influenced primarily by the nutritional content of vegetation and that herbivores select forage in an attempt to meet their nutritional requirements (Tribe 1950a; Westoby 1974; Arnold & Dudzinski 1978; Mattson 1980). Data relating diet selection to food quality come from a wide variety of studies (Weir & Torell 1959; Cowlishaw & Alder 1960; Arnold 1960a,b,1963; Arnold *et al.* 1966; Westoby 1974; Harwood 1975; Appleby 1980). The diets selected were found to be of better nutritional quality than the average for the available forage. The most widely used biochemical parameters for measuring the nutrient status of vegetation are nitrogen, fibre and carbohydrate content (Tribe 1950b; Van Soest 1982; Robbins 1983). Water content is occasionally measured (Owen *et al.* 1977), and is considered to be especially important in insect diet selection (S. Simpson pers. comm.). However, animals might be selecting for much more specific chemicals such as particular amino acids, sugars or trace elements which correlate with the presence of the chemicals detected by cruder analyses (Arnold & Dudzinski 1978). Problems of correlations between various nutritional, and allelochemical diet components, as well as physical factors make interpretation of crude chemical analyses difficult.

One important reason why selection for high nitrogen content of vegetation must occur is that herbivores have greater difficulty than carnivores in accumulating nitrogen for protein manufacture (Mattson 1980). The nitrogen content of plant material varies from 0.03-7.5 % nitrogen on a dry weight basis, whereas that of animal tissue is in the region of 7-14% (Mattson 1980). Therefore, it would be sensible for herbivores to select vegetation of highest nitrogen content. Other studies have suggested that herbivores prefer vegetation which is high in water soluble carbohydrate rather than nitrogen (Plice 1951; Cowlishaw & Alder 1960; Bland & Dent 1964; Gibb *et al.* pers. comm.).

Another possible explanation for observed diet selection is that certain plants are avoided because they contain secondary compounds such as tannins which may either have a toxic effect on the grazer or reduce the digestibility of the plant (Bryant & Kuropat 1980; Crawley 1983; Miller 1986; literature reviewed in Provenza & Balph 1987).

1.2 The role of physical constraints in diet selection

More recently, the extent to which "active" selection for high quality forage occurs in herbivores such as cattle (*Bos* spp.) and sheep (*Ovis aries* L.) has been challenged as a consequence of research examining the physical factors that influence forage intake (Allden & Whittaker 1970; Barthram 1981; Grant *et al.* 1985; Penning 1986; Illius & Gordon 1987). In sheep, bite rate decreased while bite size (the size of a mouthful of forage) increased with the height of the grass sward being grazed (Allden & Whittaker 1970; Penning 1986). In a series of painstaking experiments which involved threading individual grass tillers (plants) into holes in boards, Black & Kenney (1984) showed that the density of tillers as well as their height regulated bite size in sheep and that increased density resulted in increased bite size. Bite depth or the extent to which sheep can penetrate into a grazed ryegrass sward was also found to be dependant upon sward structure (Barthram 1981). The proportions of plant species selected by cattle grazing on Scottish hill farms was found to correlate most closely with proportions occurring in the top layer of vegetation, which constituted an "active" grazing horizon, below which the cattle did not penetrate (Grant *et al.* 1985). Thus, in order to assess the extent to which cattle were "actively" selecting forage their diets would have to be compared with the vegetation in this layer. The physical structure of the herbivore's mouth also influences intake (Illius & Gordon 1987). Smaller individuals with concomitantly smaller mouths are able to be more selective in their choice of diet than larger animals of the same species (Illius & Gordon 1987). The range of forage available to them may differ from that available to a larger animal grazing in the same environment.

The implication of this research is that physical aspects of the sward being grazed and the size of the animal are the most important factors influencing forage intake and diet selection in herbivores such as cattle and sheep (Hodgson 1982, 1984). Arnold (1960a, 1966b) recognized this when he stated that the act of grazing in sheep had both a horizontal and vertical component and that plant structure is important in determining what is available to the grazing animal. Also, Arnold *et al.* (1966) observed that sheep had a preference hierarchy of: old green leaf, green stem, dry leaf, dry stem. These conclusions may be taken one step further: grazers eat what is most easily accessible to them in the upper horizons of vegetation and this correlates with the location of the best quality forage, i.e. leaves and new growth (Hodgson 1982). Therefore, diet selection for the most nutritious forage may occur through "passive" selection.

1.3 The assessment of forage availability

Grant *et al.* (1985) demonstrated that for cattle, the "available" forage occurred in the upper horizons of vegetation. Therefore, another implication of their research, is that the way in which availability of different forage species has been assessed must be re-examined in studies in which herbivores have shown preference for different plant species, and selection correlated with food quality. In studies where the diet selected was higher in nitrogen than other available forage, one might ask whether vegetation was bulked for analysis, thereby including unavailable forage in the analysis of supposedly available material. Similarly, in studies where diet selection was apparently unrelated to food quality, was this because good forage species were lower down the sward profile and inaccessible, or because entire plants observed as being selected were analysed, rather than those parts actually selected e.g. upper leaves versus stems?

Notwithstanding, there are studies which still appear to have demonstrated selection for particular plant species or selection based on food quality regardless of the physical constraints imposed by the vegetation. These have either documented movement of animals toward good patches of forage within a stand of the same plant species (Harwood 1975; Appleby 1980) or showed that herbivores (sheep) can overcome the constraints imposed by the physical structure of the sward to get at a preferred, but relatively inaccessible species (Laidlaw 1983; Grant *et al.* 1985). In addition, there are "cafeteria trial" studies which have allowed animals equal access to different plant species or pelleted foods of different quality. This approach has been used to determine preference rankings for particular plant species. However, the results were often equivocal because preferences for particular plant species depended upon the relative abundance of other species and it was possible to obtain different species preference rankings from different trial designs (Crawley 1983). Cafeteria trials have been used most often by researchers investigating dietary self-selection: the ability of animals to choose a diet from an array of purified or natural foodstuffs that best meets its nutritional requirements (Overmann 1976). In many of the early studies with pelleted foods, the herbivores failed to select the most suitable diet (reviewed in Tribe 1950a). Suitability was defined by the ideal balanced diet required for optimal growth (Tribe 1950a). However, cafeteria trials have been criticised as being too far removed from normal feeding conditions (Tribe 1950a; Crawley 1983). Recently, dietary self-selection has been documented in lambs (Cropper *et al.* 1985).

The first two explanations of what determines diet selection in vertebrate herbivores, (a) nutritional quality of vegetation, and (b) the need to avoid toxic secondary compounds, provide functional hypotheses. The "passive" food selection hypothesis is a mechanistic, or causal explanation. However, it does give rise to an alternative functional hypothesis for explaining forage intake by herbivores. Since bite size, and therefore overall intake rate is greatly dependant on sward height and density, then herbivores feeding in an area of acceptable forage may be expected to be attracted to sites which provide them with larger mouthfuls, enabling them to maximize their intake rates of dry matter (and nutrients) (Black & Kenney 1984). As far as I know, there have been no tests of this hypothesis, although Kenney & Black (1984) showed that when penned sheep were offered the same hay chopped to different lengths, they preferred the length that resulted in their obtaining the greatest rate of intake.

1.4 Objectives of this study

All of the explanations discussed thus far probably have some validity in explaining observed diet selection in herbivores. However, they also interact with each other in varying degrees, and their relative importance is still unclear. For example, the importance of sward structure in determining diet selection in herbivores may change according to the overall nutritional quality of the vegetation. The overall objective of this study was to determine the relationship between the nutrient content of vegetation and its physical structure in influencing diet selection in a vertebrate herbivore. This was sub-divided into three main objectives:

(1) To test experimentally whether sheep select forage of better nutritional quality when physical sward parameters (height, tiller density, pseudostem and lamina length) are held constant.

(2) To determine the response of grazing sheep to variation in the visual appearance and physical structure of perennial ryegrass (*Lolium perenne* L.) swards and to investigate visual cues associated

with perennial ryegrass that sheep may use to assess its nutritional quality.

(3) To determine whether forage intake in grazing sheep can be predicted by a rate-maximizing model of optimal foraging theory.

These objectives are considered in more detail below:

(1) To test experimentally whether sheep select forage of better nutritional quality when physical sward parameters (height, tiller density, pseudostem and lamina length) are held constant.

There have been no studies which have experimentally tested the role of nutritional quality in diet selection while controlling the physical sward parameters which influence selection. Grant *et al.* (1985) demonstrated active species selection, but did not examine its nutritional basis.

Work of this sort carried out in mixed plant species community will alway be confounded by the presence of secondary compounds influencing inter-specific selection. Therefore, experiments were carried out within a monoculture of perennial ryegrass. There is enough intra-specific variation in nutritional quality of grasses (Corrall *et al.* 1979; Cargill & Jefferies 1984) to create areas of widely differing forage quality. The nutritional requirements of herbivores vary with age, season, and recent physiological condition (Ørskov 1982; Crawley 1983) and the suitability of vegetation for inclusion in diets will vary accordingly. Nutritional quality of vegetation can only be truly defined in the long term by the effect of its inclusion in the diet on an animal's growth rate and reproductive success (Crawley 1983). I have characterized nutritional quality in terms of the nitrogen and water soluble carbohydrate content and digestibility of ryegrass because the effect of various levels of these parameters in vegetation on sheep growth is known (Ørskov 1982; Van Soest 1982). Physical parameters of the sward were manipulated by varying sowing densities of seed and by clipping treatments. Sheep were selected as the study animal, for three reasons. Firstly, their grazing behaviour has been well studied and secondly, they are highly tractable animals. Finally, their nutritional requirements are well known, and provide a context in which to place biochemical measurements of perennial ryegrass.

A second aim of this study was:

(2) To determine the response of grazing sheep to variation in the visual appearance and physical structure of perennial ryegrass swards and to investigate visual cues associated with perennial ryegrass that sheep may use to assess its nutritional quality.

It is well demonstrated that the senses of touch, taste and smell are important in determining diet selection and species preferences in sheep (Tribe 1949; Arnold 1966b; Arnold *et al.* 1980). Apart from orienting the grazing animal to other sheep and its environment, Arnold (1966a) concluded that sight was not particularly important in determining plant species preferences in sheep. This conclusion was reached in spite of some experimental results indicating that blinkered sheep selected less nutritious forage than unblinkered sheep and that their mode of grazing differed considerably (Arnold 1966a). Given the excellent binocular vision of sheep (Whitteridge 1978) and their ability to discriminate among the faces of other sheep, dogs and humans (Kendrick & Baldwin 1987), it seems likely that the role of vision may be more important in diet choice than Arnold (1966a) concluded.

Research into behavioural mechanisms that sheep, and herbivores in general may use in diet selection has not extended much beyond the studies mentioned above. In particular, very little is known about the capability of herbivores to learn about forage quality with respect to its nutritional and toxic content (Westoby 1974; Provenza & Balph 1987). Rats (*Rattus* spp.) have been intensively studied and are able to select well-balanced diets, and to correct for nutrient deficiences and avoid toxins by means of a variety of behavioural and physiological mechanisms (reviewed in Overmann 1976). They incorporate small amounts of novel foods in discrete meals and are able to link adverse physiological effects with the food that caused them. This is known as long-delay learning, because the effect of a particular action may take a long time to occur but still be associated with a particular cause. It has been commonly assumed that because large vertebrate herbivores do not have discrete meals, it would be much more difficult for them learn such associations as they would be unable to link accurately physiological effects with a specific food item (Westoby 1974; Zahorik & Houpt 1981; Miller 1986). Zahorik & Houpt (1981) found little evidence of long-delay learning in ponies. However, over longer periods of time some association between general well-being and certain sensory aspects of forage must be expected to develop (Provenza & Balph 1987).

In the experiments associated with objective (2), the broad aim was to relate intra-specific diet preferences of sheep to physical aspects of the sward structure, e.g. height, and also to variation in shade and hue of vegetation. If sheep prefer vegetation that they can eat faster (Black & Kenney 1984; Kenney & Black 1984), thereby increasing their intake rate, then they may respond to a visual cue such as sward height, which is correlated with bite size (Penning 1986). Additionally, there might be other visual cues that predict nutritional quality within plant species. Since sheep apparently do not have colour vision (Tribe & Gordon 1949), then brightness was considered to be a variable to which they may respond. It is also a physical parameter which may be used to characterize ryegrass swards in addition to the other more conventional parameters, such as height. The relationship betwen variation in the brightness of perennial ryegrass and nutritional quality was investigated. In addition, experiments were designed to determine whether sheep exhibit a response to variation in the brightness of ryegrass that was in any way associated with the selection of a diet of increased nutritional quality.

1.5 Optimal foraging theory

The third overall objective of this study was:

(3) To determine whether forage intake in grazing sheep can be predicted by a rate-maximizing model of optimal foraging theory.

Over the last twenty years, a considerable amount of theoretical and experimental work has examined whether foraging animals use any general rules to determine what food to select and where and how to feed (Krebs *et al.* 1983). Optimal foraging theory (OFT) assumes that natural selection has acted on decision rules made by a foraging animal to allow it to perform as efficiently as possible (Krebs *et al.* 1983). A number of assumptions are involved in OFT and these are reviewed in detail by Pyke (1984). They may be summarized:

(a) An individual's fitness depends upon its behaviour while foraging and there is a heritable component of this behaviour.

(b) A relationship between foraging behaviour and fitness is assumed to exist and fitness is assumed to be function of some rate e.g. rate of energy intake.

There are three main groups of foraging models: (a) prey selection models, (b) patch models and (c) central place foraging models.

Prey models predict which prey items an animal should select, subject to various constraints, in order to maximize the intake rate of some currency, usually energy (Stephens & Krebs 1986). Constraints identified in these models are prey handling and search times. The model may predict, for example, that an animal should reject a very large and therefore highly nutritious prey item in favour of slightly smaller items because the big item takes five times as long to handle.

Patch models look at animals foraging in an environment in which food is patchily distributed. They make predictions about how long an animal should stay in a patch in order to maximize net gain of some currency (again, usually energy) subject to how long it takes the animal to move between patches (Krebs &

Stephens 1986). It is assumed that the rate of gain of currency declines the longer the forager stays in the patch, because food items are being depleted and therefore becoming more difficult to find. This pattern of depletion is known as the "gain function". The constraints in these models are travel time and the gain function. The longer that it takes to travel between patches, the longer the forager should stay in the patches in order to maximize its energy gain.

The prey and patch models were the first to be developed and since then other groups of models have evolved among which lies the third group. Central place foraging models were developed for animals searching for food to bring back to some central place e.g. a nest or cache (Krebs *et al.* 1983). They predict the optimal prey and load sizes as a function of how far the forager must travel from its central place. The ways in which these three groups of models have developed is reviewed by Pyke (1984) and Stephens & Krebs (1986).

The ideas and approaches embodied in OFT have generally been slow to percolate into the consciousness of both agricultural and ecological researchers examining diet selection in vertebrate herbivores. Evidence for this comes from the low number of papers that have examined this question from an OFT point of view (Westoby 1974, 1978; Belovsky 1978, 1984a, b; Owen-Smith & Novellie 1982). It is difficult to assess exactly why this is so, although the apparent rejection of OFT by some researchers as having nothing new to offer to the field, may be partly responsible. Crawley (1983, p. 168) stated that "contrary to optimal foraging theory, the diets of large, vertebrate herbivores are typically composed of many plant species". Miller (1986, p. 161) stated that his results were "contrary to conventional optimal foraging models and suggest that the assumptions of the model are not realistic for bighorn sheep and... other generalist herbivores." In addition to the failure of OFT models to accurately predict plant species included in herbivore diets (Belovsky 1981; Owen-Smith & Novellie 1982; Miller 1986) is the existence of studies documenting that vertebrate herbivores did not select the most nutritional plant species available (reviewed in Westoby 1974). Perhaps this was seen by some researchers as evidence that OFT was of little use, because it assumed that animals must select the most nutritious plant species.

The above quotations and references all refer to the prey selection group of models and Stephens & Krebs (1986) discuss how the distinctive constraints acting on herbivores, as pointed out by Crawley (1983, p. 168), may be incorporated into such models. For example, the need for herbivores to incorporate small amounts of particular species into their diets which provide essential vitamins, minerals or amino acids, or the need to track an environment in which nutritional quality is continually fluctuating. Thus, prey models may be developed which predict that herbivores should have diets that vary with respect to nutritional content of component species. In addition, it is perhaps inappropriate to expect the prey selection models to predict the exact plant species composition of diets. This presupposes that herbivores classify plants in the same way as man, as taxonomic species; they may not. Several plant species ranked by a researcher as being different may all fall into the same category from the herbivore's point of view. Also, herbivores may be unable to synthesize information about many different plant species within a particular diet class (Belovsky 1984b). It may be more sensible for herbivores to adopt a grazing strategy in which they do not always select the "best" plant in any forage class, but every food item which meets some minimum nutritional requirement (Belovsky 1984b). It seems highly likely that this sort of process may be occurring in agricultural studies carried out in well fertilised fields, in which the selected diet varies little in nutritional quality from the available forage and the best species are not preferred (Bland & Dent 1964; Buckner *et al.* 1967).

Stephens & Krebs (1986) have pointed out that patch-use models may be more useful and appropriate than the prey models in studies of herbivory. Foraging animals are expected to leave patches before consuming all available food - something that herbivores do. Also, food items encountered and eaten by herbivores are not discrete in the sense envisaged by the prey models (Stephens & Krebs 1986). To my knowledge, patch models have only been used in one herbivory study (Parker 1984), which showed that grasshoppers stayed in patches for longer when their inter-patch travel time was increased.

Patchiness may exist at a wide variety of levels for herbivores:

(1) Habitats e.g. woods, open grasslands.

(2) Species composition within a plant community.

(3) Nutritional variation within a species e.g. new leaves versus old leaves on a plant.

(4) Structurally e.g. tall versus short plants, bushes versus trees.

Belovsky (1978) predicted the optimal time allocation for a moose (*Alces alces*) between aquatic and terrestrial habitats in order to meet its energy requirements and satisfy its demand for sodium. His observations fitted well with his predictions. This type of analysis considers patchiness on a very large scale. Although acknowledged as existing (Arnold & Dudzinski 1978; Crawley 1983), the basis of within-plant selection has been little studied in vertebrate herbivores and little is known about how this level of patchiness is perceived. Thus, the third aim of this research was to determine whether forage intake in grazing sheep could be predicted by a patch use model, the marginal value theorem (Stephens & Krebs 1986), on a finer, intra-specific level within a ryegrass monoculture. Results from earlier experiments were used to define what sheep perceived a "good" patch of ryegrass to be. Thus, by identifying intra-specific preferences, nutritionally and structurally good patches were created in a background sward of poor, less acceptable ryegrass. Travel times of sheep between good patches were varied and their observed times spent grazing in these patches were compared with predicted times obtained from experimentally determined intake curves of ryegrass biomass.

Diet selection in vertebrate herbivores grazing in multi-species plant communities will be affected by complex interactions between secondary plant compounds, intra- and inter-specific variation in nutritional quality of vegetation as well as its physical structure. These interactions will be such, that the relative importance of any one of these variables in influencing diet selection must be difficult to evaluate. By investigating the basis of diet selection in sheep grazing within a monoculture of an acceptable forage species, the variables inflencing diet selection were greatly simplified. This allowed behavioural responses of sheep to be more clearly evaluated. In addition, the patch-use models of optimal foraging theory have been used to examine behaviour of sheep in this simplified grazing environment.

Chapter 2

The effect of nutritional and structural variation in perennial ryegrass swards on diet selection in sheep assessed by the transplanted turf method

2.1 Introduction

Although at one point it was thought that herbivore populations might not be food limited, since the world is essentially green (Hairston *et al.* 1960), not all vegetation is available or acceptable as forage (Sinclair 1975; Van Soest 1982; Crawley 1983). Not only do some plants contain toxic compounds (Crawley 1983), but there is a wide range of nutritional quality both between and within species (reviewed in Mattson 1980; Allden 1981; Hacker 1982).

The notion,that there may be a nutritional basis to diet selection by vertebrate herbivores,is supported by observations of this sort,and also from agricultural research demonstrating that there are nutritional thresholds which must be met in order for individual herbivores to survive. Sheep and cattle require a minimum level of nitrogen in the diet for maintenance of rumen microflora populations (Allden 1981; Simpson & Stobbs 1981; Van Soest 1982). In many tropical pastures for example, the minimum values of the range of nitrogen content of vegetation often fall well below these levels (Allden 1981). The growth and reproduction of ruminants is also limited by the digestibility of available vegetation (Freer 1981; Van Soest 1982) and by levels of specific nutrients such as sodium (Belovsky 1978) and phosphorus (Van Soest 1982) in plants. Therefore, the process of natural selection must have ensured the survival of individuals selecting adequate diets.

It may be hypothesized that individuals with particular foraging behaviours which determined diet quality were favoured. A key assumption of optimal foraging theory is that individuals should be selected to maximize their rate of nutrient intake which is assumed to be related to overall fitness. However, there is very little empirical information from wild populations on the relative fitness of herbivores feeding on vegetation of different nutritional quality and on differences in foraging behaviour which may have resulted in diets of different nutritional quality being ingested (Tuenissen *et al.* 1985; Iason *et al.* 1986). One example is the Red deer (*Cervus elaphus*) population on the Isle of Rhum, Scotland, where the reproductive success of hinds grazing on grass enriched with nutrients, particularly nitrogen, and probably calcium (P. J. Ewins pers. comm.), from gull droppings was greater than that of hinds grazing in lower quality grass areas (Iason *et al.* 1986). Also, more dominant stags preferred to feed in grass areas that had been artificially fertilised, and displaced subordinate animals in order to do so (Appleby 1980).

Many studies have attempted to determine whether vertebrate herbivores actively select vegetation of the highest available nutritional quality relative to the range available (Table 2.1). A number of non-ruminant herbivores such as geese and monkeys have been shown to select forage of higher nitrogen content than background levels present in forage species. In all field studies of wild ruminants the diets selected were explained by nutritional requirements (Table 2.1). Although it has long since been concluded that sheep and cattle select diets higher in nitrogen and digestibility than background swards (Fontenot & Blaser 1965), in only one field study described in Table 2.1, was it made clear whether more nutritious vegetation was concentrated at the top of the sward (Alder & Minson 1963). This is usually the case in pastures (Arnold 1960a; Alder & Minson 1963; Burton *et al.* 1964). In experimental studies, variation in physical sward factors such as tiller density, total biomass, and sward height were not controlled or measured (Table 2.1). Hardison *et al.* (1954) considered that these sorts of factors may also have been influencing selection. In only three studies were results indeterminate (Warnke *et al.* 1952; Bland & Dent 1964; Buckner *et al.* 1967), and it was also the case that physical factors were not controlled or measured.

Two experiments were carried out to investigate the relative importance of the effect of sward structure on diet selection in sheep. The objective of the first experiment was to determine the response of sheep grazing swards of ryegrass which contained patches of higher nutritional value, but of structural similarity to the background sward. This approach was different from previous studies which found the quality of sheep diets to be higher than that of the available vegetation. I wished to discount the "passive selection hypothesis" which explains sheep diets purely in mechanical terms, as a result of their removing the top layer of vegetation which is correlated with the location of the new and more nutritious growth (Arnold 1960a, 1966b; Hodgson 1982, 1984; see Chapter 1). In my experiments, sheep were required to actively locate good patches of vegetation in order to improve their diet quality.

The objective of the second experiment was to determine the response of sheep to two types of ryegrass patch: one taller than the background sward and one trimmed to the same height as the background sward. Both types of patch were of higher nutritional quality than the background sward.

The main criterion of nutritional quality was the nitrogen content of ryegrass. Good patches were fertilised while the background sward was not. Thus, I assumed that the general grazing environment would be poorer than was normally the case on intensive farms. Fertilisation does not have a predictable effect on

Table 2.1. Studies examining the nutritional basis of diet selection in vertebrate herbivores.

Authors	Species	Type of study*	Basis of assessment	Result	Choices of diet equally available?†	Physical sward parameters controlled?††
Harwood 1975	Lesser snow goose	E	Feeding time	Preferred fertilised swards of grass	Yes	Height only
Owen *et al.* 1977	Barnacle goose	E	Feeding time & intake (no. of pecks)	Preferred fertilised grass trays and high water content	Yes	Yes
Tuenissen *et al.* 1985	Brent goose	F/E	Feeding time & breeding success	Preferred fertilised grass. Females feeding on high quality species had higher breeding success	Yes	No, greater biomass on fertilised salt marsh plots
Clutton-Brock (Ed.) 1977	Various primates	F	Analyses of food plants selected and rejected were compared with estimates of nutritional requirements	Selected young leaves rich in protein and carbohydrate rich fruit. Appeared to select balanced diets	Apparently	No
Glander 1981	Mantled howling monkeys	F	Time spent feeding in various trees. Nutrient levels of preferred and avoided leaves compared	Same as above	Yes - monkeys were highly moblile	No

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* F = field, E = experimental, F/E = manipulations of forage under field conditions

† High quality vegetation may have been concentrated in the upper sward horizons

†† Gives details of whether physical parameters were considered and controlled

Authors	Species	Type of study*	Basis of assessment	Result	Choices of diet equally available?†	Physical sward parameters controlled?††
Sinclair 1975	African ungulates	F	Compared chemical analyses of young, preferred leaves with older leaves on same bush	Selected leaves of greater crude protein content	Don't know	No
Belovsky 1978	Moose	F	Time allocation	Moose allocated time as predicted in aquatic habitats to meet estimated sodium requirement	Don't know	No
Price 1978	Coke's Hartebeest	F	Quality of observed diets and generally available forage was compared with maintenance requirements	Diet selected was higher in protein and digestibility and met maintenance requirements whereas unselective diet did not	Probably not	No
Appleby 1980	Red deer	F/E	Feeding time	Preferred fertilised *Agrostis/ Festuca* swards	Yes	No, greater biomass on fertilised plots, which were also taller
Weir & Torell 1959	Sheep	F/E	Comparison of oesophogeal fistula samples with handclipped samples	Observed diet was higher in nitrogen and lower in fibre	Probably not	No

Authors	Species	Type of study*	Basis of assessment	Result	Choices of diet equally available?†	Physical sward parameters controlled?††
Arnold 1960b	Sheep	F	Oesophageal fistula samples compared with apparently bulked vegetation	Observed diet was higher in nitrogen	Probably not	No
Arnold *et al.* 1966	Sheep	F	"	Observed diet was higher in green leaf material than pasture	Probably not	No
Hamilton *et al.* 1973	Sheep	F	"	Observed diets higher in digestibility when biomass >50 g m^{-2}	Probably not	No
Warmke *et al.* 1952	Cattle	E	Intake from sown plots	Variation in water soluble sugars did not explain preferences for different spp. of tropical legumes. Nitrogen not analysed.	Yes	No
Cowlishaw & Alder 1960	Cattle/sheep	E	Intake from sown plots estimated by eye	Preferred plots of grass spp. higher in water soluble carbohydrates	Yes	No
Bland & Dent 1964	Cattle	E	"	Preferred varieties of Cocksfoot grass higher in sugars and digestibility	Yes	No

Authors	Species	Type of study*	Basis of assessment	Result	Choices of diet equally available?†	Physical sward parameters controlled?††
Bland & Dent 1964	Sheep	E	"	No relationship between varietal preferences and nutritional parameters (biochemical analyses)	Yes	No
Reid *et al.* 1967	Sheep	E	Intake assessed by before and after comparisons of vegetation in plots	Preference for fertilised plots of Fescue	Yes	No
Blaser *et al.* 1960	Cattle	F	Liveweight production of cattle grazing top and bottom of sward	Observed diet was higher in nitrogen and lower in fibre	No	No
Hardison *et al.* 1954	Cattle	F	Diet estimated by faecal analysis was compared with bulked herage	Observed diet was higher in crude protein and digestibility than available forage	Probably not	No
Arnold 1962	Sheep	F	"	Observed diet was higher in digestibility	Probably not	No
Alder & Minson 1963	Cattle	F	Herbage collected from different sward horizons was compared with diet estimated by faecal analysis	Diets selected from top 4" of sward was higher in digestibility than herbage from lower sward horizions	No	Yes, sward hts measured before & after grazing. Herbage collected in stratified layers

Authors	Species	Type of study*	Basis of assessment	Result	Choices of diet equally available?†	Physical sward parameters controlled?††
Buckner *et al.* 1967	Cattle	E	Unclear	Some preference for varieties higher in sugar and digestibility, lower in silica content Nitrogen did not differ between plots	Yes	No

digestibility of forage (Binnie *et al.* 1974; Van Soest 1982), although a number of authors suggest that nitrogen content of vegetation is correlated with digestibility (Tribe 1950b; Belovsky 1981; Owen-Smith & Novellie 1982). By using young ryegrass to form good patches, I expected that fibre levels would be lower than in the background sward. Thus, I planned to manipulate the two most important general criteria of ruminant nutrition (Ørskov 1982; Van Soest 1982). The sheep were apparently not limited by other nutritional requirements such as copper or phosphorus, because they had been given supplementary minerals if and when required (C. Howes pers. comm.).

2.2 Responses of sheep to nutritional variation in structurally homogeneous perennial ryegrass swards created by transplanting turves into the sward

2.2.1 Methods

General background

The experiments described in this chapter and in chapters 3 and 4 were carried out in four 25 m x 25 m paddocks linked by a central gateway, at the Oxford University Field Station, Wytham, Oxfordshire (51° 47' N, 1° 19' W). All references to specific paddocks in this and other chapters refer to the numbered arrangement given in Figure 2.1. Where times of day are given in the text, they refer to British Summer Time. Times of day given for experiments carried out on dates when clocks had reverted to Greenwich Mean Time include the equivelant in British Summer Time in parentheses.

The paddocks were sown with *Lolium perenne* var. Melle (perennial ryegrass) in April 1985 at a rate of 25-30 kg seed/hectare. They were not fertilised at the time of sowing and received no fertiliser during the following three years except in the case of specific experiments in which fertilisation was highly localized (see Chapter 3). In addition they were heavily grazed and mowed. My aim was to reduce the nutrient status of the sward and to maintain a sward in which there was as little dead material as possible. In June and early July 1985, the paddocks were mowed every 2-3 weeks with a small tractor mower and all cuttings were removed Until mid-August they were periodically stocked with cross-bred Mule (Swaledale x Border Leicester) ewes, which kept the sward grazed down to a height of approximately 5 cm.

Appendix 2.1 contains a glossary of botanical terms relating to grass morphology and other aspects of grass farming, which appear frequently in the text.

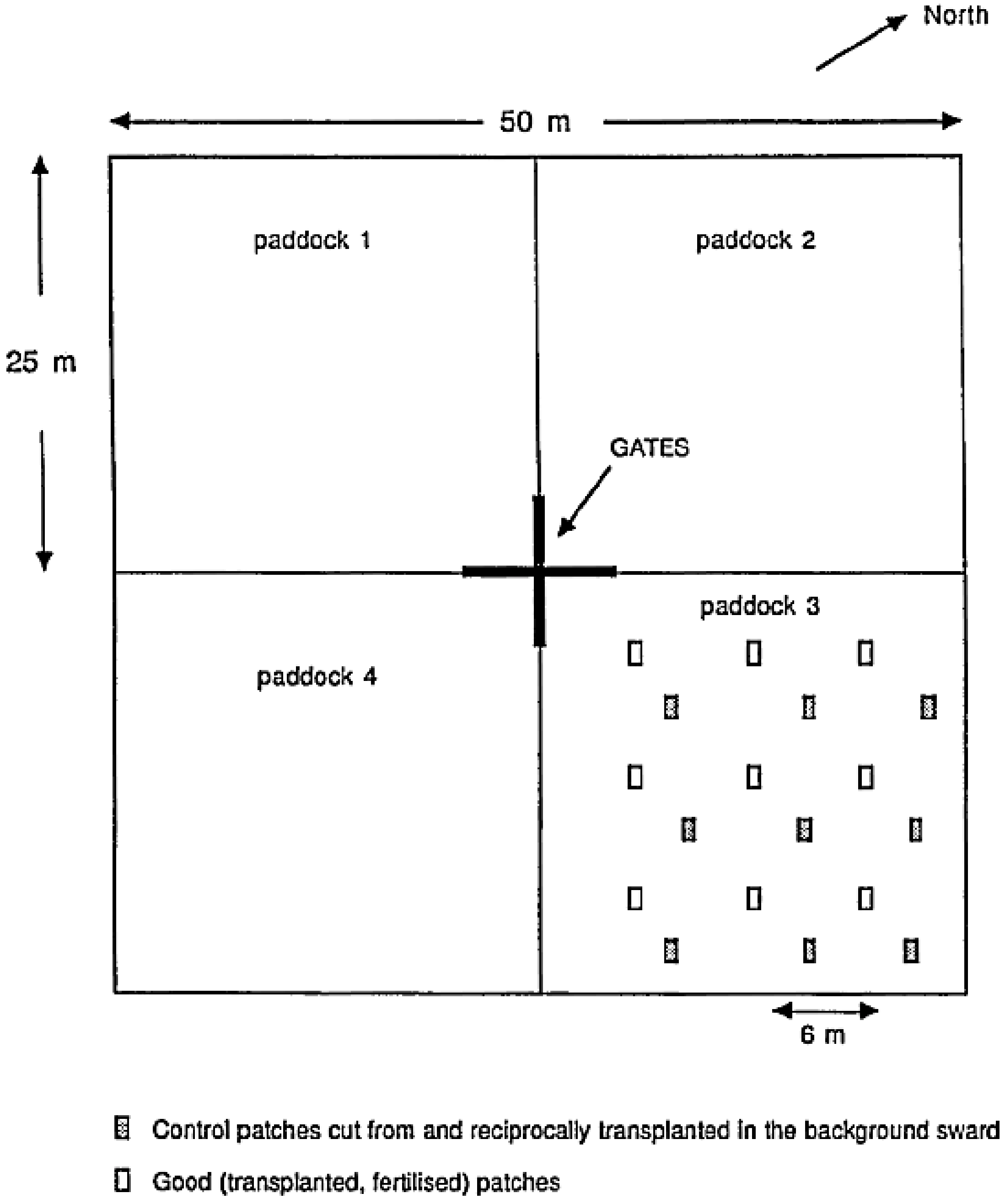

Figure 2.1. Arrangement of paddocks and patches used in experiments.

1985 Experiments

In order to maintain as homogeneous a sward as possible, the paddocks were mowed from mid-August and throughout the experimental period in 1985. In July 1985, nine shallow holes, approximately 5 cm deep and 40 x 70 cm in area were dug in each of paddocks 1, 2 and 3. The holes were arranged in a 3 x 3 grid and were approximately 6 m from each other (Figure 2.1).

Turves of ryegrass, which were to be transplanted into these holes to create nutritionally good patches, were planted in August and September 1985. Five groups of 40 trays (each tray: 21 x 35 cm) were sown with perennial ryegrass seed var. Parcour at 0.5 g seed/tray (Table 2.2). A different variety of ryegrass was used for turves, because in greenhouse trials conducted in April 1985, in which growth of five varieties of perennial ryegrass was compared, Parcour was the fastest growing. Therefore, turves of a particular height could be obtained faster than with other varieties, such as Melle. Trays were fertilised on two occasions with Maxicrop liquid fertiliser and they were approximately one month old when used in experiments.

Two days before each experiment, the paddock to be used was mowed to a uniform height between 5 - 8 cm. The following day, four sward height measurements were taken at each of 27 points selected at random in the paddock and a mean sward height calculated (n = 108). All sward height measurements were taken with a sward stick made in the Department of Zoology, Oxford University, to Hill Farming Research Organisation specifications (J. Hodgson pers. comm.). The turves grown up in trays were then trimmed to this mean height with sheep shears and transplanted into each shallow hole. They were held in place with metal skewer type tent pegs. Four turves fitted into one hole, and 36 of the 40 turves in a group of the same age were used for each experiment. Thus, there were nine nutritionally good patches, each measuring 40 x 70 cm. Reasons for the choice of patch size are discussed in section 2.4. Each good patch was marked with a white bamboo pole approximately 50 cm long, which allowed an observer to locate it rapidly. In order to control for the sheep being attracted by bamboo poles, two other poles were placed at random 2 - 3.5 m from each patch.

The latter two of the five experiments run in 1985 incorporated a major modification to the experimental design. In addition to transplanted turves grown in trays, nine patches were created from turves cut from the background sward and then reassigned at random to the regularly dispersed locations from which they had been cut (Figure 2.1). These patches were of similar size to those comprised of turves grown in trays, and they controlled for sheep being attracted by freshly disturbed soil. Turves in these "control" patches were switched on the day preceeding each experiment. They were also marked with bamboo poles.

Table 2.2. Ages and sowing dates for turves of perennial ryegrass (variety Parcour) transplanted into paddocks as good patches.

Sowing date	Amount of seed (g/tray)	Date of experiment	Age of turves at use (days)
1985			
2 August	0.5	2 September	32
7 August	0.5	6 September	33
14 August	0.5	14 September	31
21 August	0.5	4 October	44
30 August	0.5	15 October	46
1986			
1 June	1.2	9 July	39
1 June	1.2	15 July	45
17 June	1.2	22 July	35

An experiment took one day to complete and five were run in September and October 1985. Each experiment started between 09:20 and 10:20, when a group of three ewes was admitted to the paddock and they were removed 3 - 6 hours later (Table 2.3). Groups of three ewes were used because I had been advised that this was the smallest group size in which grazing behaviour would not be different from that of sheep in a flock (J. Hodgson pers. comm.). In larger groups it would have been more difficult to observe the behaviour of focal animals continuously. One group of sheep was tested on three experimental days, while a second group was tested in two experiments (Table 2.3).

Measurements of sward height were used to detect changes in the transplanted patches relative to the background sward. The use of ryegrass sward height measurements to detect grazing pressure on swards and to give an indication of biomass present has been recommended by reseachers at both Hill Farming Research Organisation and Animal and Grassland Research Institute (J. Hodgson, T. Parsons pers. comm. see also Hodgson *et al.* 1986).

In the first three experiments, six sward height measurements were taken in the following three types of site:

(1) In each transplanted patch.

(2) In a 50 x 50 cm area close to one of the bamboo poles placed in the back ground sward 2 - 3.5 m from each patch.

(3) In a 50 x 50 cm randomly selected area 2- 3.5 m from each patch unmarked by any bamboo pole.

Each set of measurements was taken immediately before and after each experiment and once or twice while the sheep were grazing the paddock. In the final two experiments, measurements of the transplanted patches cut from the background sward and designated as control patches were also made.

Behavioural observations consisted of 15 minute periods during which focal sheep were scored every 30 seconds for whether they were grazing in a transplanted good patch or elsewhere in the paddocks.

Data were collected on additional parameters of sward structure: pseudostem and lamina lengths, tiller density and biomass, and vegetation was analysed for nutrient content. On the day following each experiment three of the four remaining turves which had not been tranplanted were sampled. Live biomass was carefully removed by clipping tillers at the soil surface. Tiller density was measured by counting all tillers in a turf. Pseudostem and lamina lengths were estimated by measuring six tillers selected at random from each turf (see Appendix 2.1 for definitions). The biomass was washed over a sieve and dried at 80°C. It was analysed for

Table 2.3. Summary of experimental designs used in grazing experiments which investigated the response of sheep to good patches of perennial ryegrass.

Date	Start Time	Finish Time	No. of Good Patches	No. of Control Patches	Sheep
<u>1985</u>					
2 Sept.	10:20	14:15	9	-	266, 224, 234
6 Sept.	09:20	15:15	9	-	"
14 Sept.	10:20	14:15	9	-	"
4 Oct.	09:25	15:00	9	9	267, 215, 252
15 Oct.	09:30	16:20	9	9	"
<u>1986</u>					
2 July	06:00	19:30	0	9	266, 267, 224
9 July	06:00	15:00	9	9	"
12 July	06:00	15:30	0	9	"
15 July	06:00	18:00	9	9	"
18 July	06:00	15:00	0	9	"
22 July	06:00	15:30	9	9	"

total nitrogen and modified acid detergent fibre (Appendix 2.2). A modified golf-hole corer (diameter approx. 10 cm) was used to sample 27 cores from paddock 2 in October 1985. Three cores were taken at distances of 1-3.5 m in random directions from the location of each "good" patch. This resulted in the systematic and comprehensive sampling of the entire background sward. Live biomass was removed and treated as described above.

1986 Experiments

In July 1986, six experiments were run in paddock 1 with three ewes used in 1985 (Table 2.3). From early spring to early May 1986 the paddock was heavily grazed to a height of less than 5 cm. Thereafter, it was allowed to grow up and mowed every 2-3 weeks until used, when it was about 10 cm in height. A similar experimental procedure to 1985 was followed, involving the use of transplanted good and rotated control patches, except that on every other experimental day, only control patches were present. This was done in order to determine whether the behaviour of sheep differed in the presence and absence of good patches.

Experiments commenced at 06:00, because of the extremely warm weather (≥ 20°C) which resulted in reduced grazing time during the day. Experiments were run until each sheep had grazed for 200 - 300 minutes. The sheep were observed continuously and time budget data were recorded as to whether each animal was grazing, standing still and ruminating, or sitting/lying down. Sward height measurements, and data from at least four 15 minute observation periods on each of two focal sheep were collected on each experimental day. On days without good patches, the 15 minute observation periods were used to record the location of focal sheep within grid squares of the paddock at 30 second intervals. The fence poles of the paddock, which were spaced at 3 - 5 m intervals, were painted with numbers and letters easily visible to an observer sitting in an adjacent paddock. Thus, it was possible to specify the location of a sheep within an area occupying 2-3% of the total paddock area. This allowed the time spent in different areas of the paddock to be compared between days with and without good patches.

In addition the same two sheep were observed for three to seven 10 minute periods during each experiment and data on sequences of steps and bites were collected on tape with an Olympus microcassette recorder. An entire step involving the movement of both front legs was denoted by "s" on the tape, and these were differentiated from "half-steps", involving the movement of one leg between groups of bites. Bites were counted in groups of five bites, and denoted by a "b" on tape. Therefore a written sequence of observations taken from a tape might have looked like:

"bbbbsssssbbsb/bbbssbbsbb/b/b/. . . ."

where slash symbols denoted half steps.

The water soluble carbohydrate content and standing crop of of good patches and the background sward in the paddock was estimated in 1986 in addition to other physical and chemical sward characteristics. Details of experiments carried out in 1985 and 1986 are summarized in Tables 2.2 and 2.3.

Calculations

Statistical analyses presented in this thesis generally followed the methods of Sokal & Rohlf (1981) and where required, made use of tables in Rohlf & Sokal (1981). Throughout the text, the word "significant" was always used in a statistical sense. Asterisks have been used to denote the following significance levels:

*	$P \leq 0.05$
**	$P \leq 0.01$
***	$P \leq 0.001$

2.2.2 Results

Physical, chemical and nutritional characteristics of good patches and background sward

The mean sward height of the paddocks at the start of each experiment varied from 5.2 - 10.2 cm (Table 2.4). In only one experiment, 15 October 1985, was the mean paddock height significantly different from the mean height of the good patches, and then only by 0.6 cm. Sward height variation within a paddock was caused by undulations and some ruts in the ground, over which the mower did not move evenly. At the start of each experiment, the mean heights of the nine marked individual 50 cm x 50 cm background areas within a paddock varied by 2-3 cm, while the difference among the mean heights of the good patches was in the order of 0.5-1.5 cm. To the human eye, the good patches were not noticeably taller than the surrounding sward.

Although the overall paddock height declined in 1986 as a result of mowing, grazing and repeated experiments in the same paddock, the 2 - 7 day gaps between experiments allowed the sward to recover. Thus, the overall decline amounted to only 2 cm. In 1985 paddocks 2 and 3 were less heavily used so the continual decline in height did not occur.

The overall height of control patches tended to be slightly lower than good patches, but these differences

Table 2.4. Mean heights of good and control patches of perennial ryegrass and the background sward in the paddocks prior to the start of each experiment.

Date	Mean height of ryegrass (cm)					
	Good Patches		Control Patches†		Paddock†	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
1985						
2 September	6.3	0.19	-	-	6.3	0.29
6 September	5.5	0.06	-	-	5.2	0.30
14 September	6.0	0.08	-	-	6.0	0.32
4 October	6.2	0.08	5.4***	0.20	6.4	0.29
15 October	6.6	0.09	5.9***	0.19	7.2*	0.28
1986						
2 July	-	-	9.5	0.27	10.2	0.26
9 July	9.9	0.08	9.6	0.26	9.6	0.20
12 July	-	-	8.8	0.21	9.1	0.24
15 July	8.8	0.08	8.0***	0.20	8.7	0.22
18 July	-	-	7.6	0.20	8.1	0.26
22 July	8.1	0.10	7.9	0.21	8.3	0.22

$n \geq 54$ for all means because sward heights taken in patches were pooled: minimum of 6 height measurements in each of 9 patches of each type.

†The mean height of each group of control patches or the background sward was compared with that of transplanted good patches using an unpaired two sample t-test.

were generally not significant and amounted to 1 cm at most.

In 1985, it was only possible to sample one paddock for its physical and chemical characteristics. As both paddocks 2 and 3 had been similarly treated, it was assumed that results from paddock 2 would be representative of paddock 3. The pseudostem lengths of transplanted turves used in paddock 3 were similar to those of sample cores from paddock 2, while turves transplanted into this paddock were up to 1.3 cm greater (Table 2.5). Lamina lengths of turves and paddock samples varied from 33 - 50 mm, and those of the paddock samples were the longest (Table 2.5). Tiller density was greatest in the paddock. Transplanted turves used in October 1985 had a higher tiller density, because they were older, and therefore more tillers developed. However, pseudostem length also increased with age.

In 1986 there was a better agreement between the structural characteristics of transplanted turves and paddock 1 (Table 2.5). Tiller density of turves was increased by sowing a greater amount of ryegrass seed. While there were some significant differences between ryegrass from turves and the paddock in pseudostem and lamina lengths, mean values were always within 1 cm. There was a large difference between the live standing crop (g dry weight m^{-2}) of transplanted turves and the paddock. This was due to the lower tiller density of turves and also to their higher water content, expressed as a percentage of fresh weight of biomass (fwt): paddock 13 July - 73% fwt, n = 24; paddock 19 July - 65% fwt, n = 18; transplanted turves - 81% fwt, n = 8.

Statistical comparisons shown in Table 2.5 were based on comparisons of good patches with those of the background sward in the paddock measured on the date nearest to when experiments were run using one-way ANOVAs. When required, data were log-transformed to meet homogeneity of variance criteria and normality of distribution. Pairwise comparisons were based on minimum significant differences for unequal sample sizes.

Results of chemical analyses indicated that nutritional value of transplanted turves grown in trays was better than that of the background swards in the paddocks. The total nitrogen content of ryegrass in the paddocks in 1985 and 1986 was lower than that of transplanted turves, although this difference was not always significant (Table 2.6). The total nitrogen content of the paddock vegetation decreased from 2.1% to 0.8% (1985 to 1986) as the sward grew older and was more heavily grazed. There was large variation between years and among groups of turves grown in the same year in the effect of the Maxicrop liquid fertiliser on nitrogen content. This was most likely due to variation in dilution of the fertiliser prior to application, and to variation in the amount that different groups of trays received. In future experiments, granular fertilisers were

Table 2.5. Structural and morphological characteristics of good patches and the background paddock sward.

	Pseudostem Length (mm)†		Lamina Length (mm)			Tiller Density (x 10^3 m^{-2})			Live standing crop (g dwt m^{-2})††	
Date	$\overline{X}$	SE	$\overline{X}$	SE	n	$\overline{X}$	SE	n	$\overline{X}$	SE
1985										
<u>Good patches</u>										
2 September	22.0	1.0	45.2	3.1	18	5.8*	0.1	3	-	-
6 September	22.9	0.9	37.9*	2.2	18	8.9	0.2	3	-	-
14 September	22.9	1.1	35.1*	2.1	18	6.2*	0.4	3	-	-
<u>Paddock 2</u>										
7 October	26.6	1.1	50.1	2.3	81	13.4	1.3	27	-	-
<u>Good Patches</u>										
4 October	33.8*	1.5	41.1	2.4	18	8.8	0.3	3	-	-
15 October	39.7*	2.5	33.7*	3.0	15	10.8	0.1	3	-	-
1986										
<u>Paddock 1</u>										
13 July	24.6	1.3	73.8	1.3	162	15.4	1.1	27	328	25
19 July	22.9	1.0	68.4	1.7	108	18.1	1.3	18	258	24
<u>Good Patches</u>										
9 July	17.3*	1.1	83.2*	2.7	18	11.5	0.4	3	108*	4
15 July	23.2	1.3	80.3	2.1	18	14.4	0.5	3	149*	7
22 July	29.1*	1.3	62.6	4.3	12	10.7*	-	2	98*	-

*Asterisks denote significant differences at $p = 0.05$ for the following comparisons: physical parameters of good patches were compared with those of the background sward in the paddock measured on the date nearest to when experiments were run. In 1985, data for good patches used in experiments in September were compared with background sward data from paddock 2.

†Sample sizes equal to those for Lamina Length.

††Sample sizes equal to those for Tiller Density.

Table 2.6. Chemical characteristics of good patches and the background paddock sward.

	Total Nitrogen (% dry weight)			% Modified Acid Detergent Fibre			Estimated Digestibility (% DOMD†)	Water Soluble Carbohydrate (mg/g dwt)		
Date	X̄	SE	n	X̄	SE	n		X̄	SE	n
1985										
<u>Good patches</u>										
2 September	4.2*	0.4	3	28.4	2.6	3	69.5	-	-	-
6 September	2.9*	0.5	3	21.5*	2.4	3	75.2	-	-	-
14 September	3.1*	0.1	3	25.9	2.0	3	71.6	-	-	-
<u>Paddock 2</u>										
7 October	2.1	0.4	25	29.1	0.8	20	68.9	-	-	-
<u>Good Patches</u>										
4 October	2.9*	0.2	3	29.9	1.9	3	68.3	-	-	-
15 October	2.5	0.2	3	31.2	1.2	2	67.2	-	-	-
1986										
<u>Paddock 1</u>										
13 July	0.7	0.05	27	26.6	0.5	27	70.9	245	8.9	27
19 July	0.8	0.04	18	23.5	0.4	18	73.5	335	8.4	18
<u>Good Patches</u>										
9 July	1.4*	0.07	3	18.8*	0.3	3	77.4	292	6.1	3
15 July	1.0	0.06	3	20.6*	0.5	3	75.9	295	4.9	3
22 July	1.2*	0.02	3	20.6*	0.4	3	75.9	270*	3.1	3

*Asterisks denote significant differences at $p = 0.05$ for the following comparisions: physical parameters of good patches were compared with those of the background sward in the paddock measured on the date nearest to when experiments were run. In 1985, data for good patches used in experiments in September were compared with background sward data from paddock 2.

†Digestible organic matter as a percentage of dry matter. Based on mean MADF value.

used, which allowed better control of bulk applications.

In 1985 there was little difference between the fibre content of good patches and the paddock sward, except for the group used on 6 September (Table 2.6). However, in 1986, good patches not only had higher nitrogen content, but also significantly lower fibre content. It was possible to express the mean modified acid-detergent fibre (MADF) content in terms of digestibility (digestible organic matter as a percentage of dry matter - DOMD). A regression equation based on *in vivo* determinations of digestibility of fresh forage grasses eaten by sheep was used (Barber *et al.* 1984) in which:

$$\% \text{ DOMD} = 98.20 - 0.820 \text{ MADF } \%,$$

Thus, the good patches tended to be more digestible than the background sward.

There was relatively little variation in water soluble carbohydrate content of ryegrass measured in 1986 (Table 2.6). Statistical comparisons between chemical characteristics of good patches and paddock ryegrass were made on either untransformed or log-transformed data with one-way ANOVAs. Pairwise comparisons were based on minimum significant differences calculated by the T-method (Sokal & Rohlf 1981).

In summary, while the sward heights of good patches and paddock ryegrass were successfully controlled (Table 2.4), in some experiments there were differences in other physical sward characteristics. Lamina and pseudostem lengths in good patches were both shorter and longer than those of the background sward depending upon the experiment (Table 2.5). However, mean values were generally within 1 cm of each other except for lamina lengths in 1985 which were up to 1.5 cm shorter in good patches. Tiller density was the most difficult physical parameter to control and it was consistently lower in good patches than in the background sward. Good patches were nutritionally better than the background sward in terms of nitrogen content and digestibility.

Effect of grazing by sheep on sward height

The response of sheep to the nine transplanted good patches was assessed in two ways: by tracking the changes in sward height of different parts of the paddocks and by direct observation of their behaviour. In all experiments, all sheep in a group visited good patches. The mean heights of each patch declined at a greater rate than those of control patches cut from the paddock and switched around, and those of sites in the background sward. Since trends were similar in all experiments, one set of results from 9 July 1986 have been presented (Figure 2.2). Within the first hour of grazing time in each experiment all transplanted patches

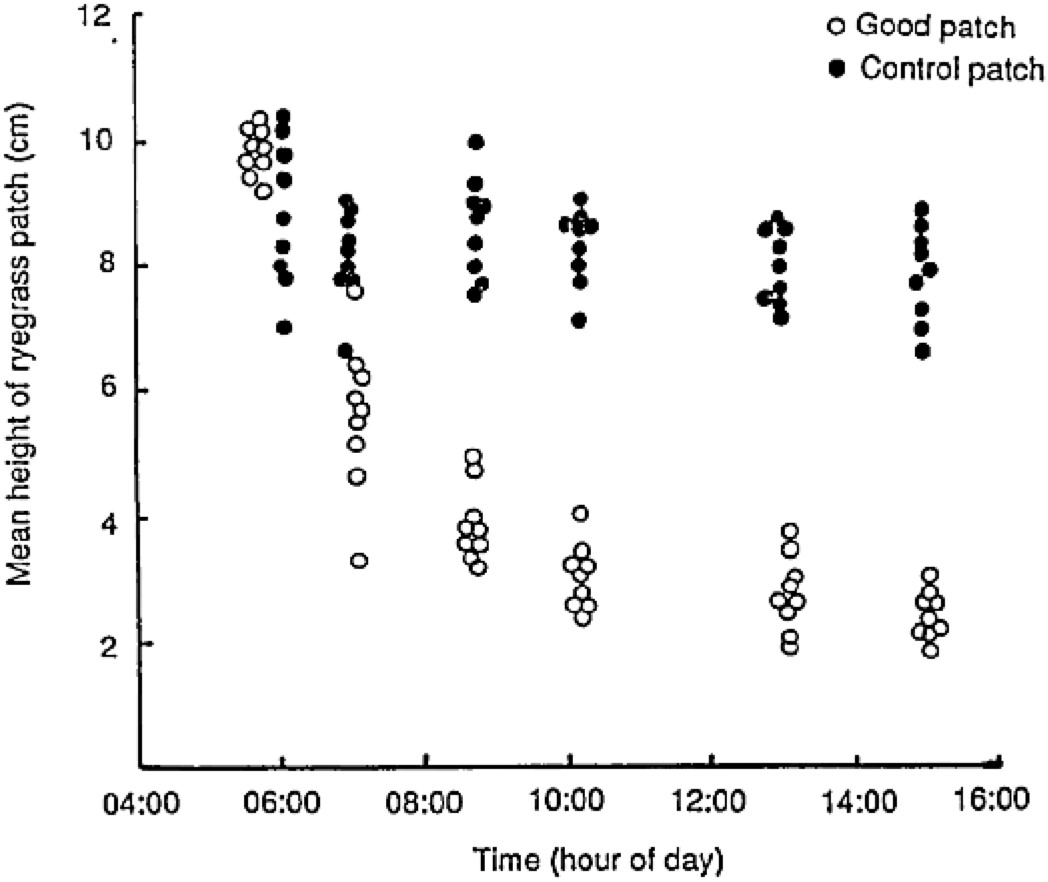

Figure 2.2. Mean sward heights of patches of perennial ryegrass grazed by sheep on 9 July 1986. (○ Good patch, ● Control patch. Each point represents the mean sward height of one patch, n = 6 sward heights per patch.)

were visited at least once, and the mean height of each good patch declined from 20-60%. Thereafter the rate of decline decreased, and the final mean height of each good patch varied from 2-4 cm. This range of final heights taken after the experiment was terminated was similar for all experimental days. By comparison, the height of the control patches declined much less.

Sward height data from all experiments are summarized in Figure 2.3. The difference in the mean sward height (cm) of each patch prior to and after each experiment ended has been calculated and a mean value taken for each group (n = 9 patches for each bar in a histogram). These values were compared with one-way ANOVAs for each experimental day, and pairwise comparisons were based on Fisher's protected least significance differences (PLSD).

There was no significant difference in the mean decrease in sward height for areas of the background sward either marked with a bamboo pole or left unmarked in any experiment in September 1985 (Figure 2.3a). Therefore, it was concluded that sheep were not attracted to graze in particular sites specifically by the presence of white bamboo poles.

In all experiments with transplanted good patches, the decrease in their height was significantly greater than that of control patches or areas of the background sward marked with bamboo poles (Figure 2.3). As sheep revisited good patches, they became more even in height. Thus, by the end of each experiment there was as little variance in height within each good patch as at the start of the experiment when they had been trimmed to a constant height.

There was no significant difference between the control patches and the background sward, except on 9 July (Figure 2.3 d).

Grazing behaviour of sheep

In 1985, experiments were run for 5-7 hours, but the sheep did not graze continuously during this time. They often sat or lay down to ruminate, and spent approximately 60% of the time grazing.

In 1986, grazing patterns were charted more accurately (Figure 2.4). There was an early morning grazing period that coincided with the start of each experiment, followed by a break of one to two hours when the sheep stopped grazing and ruminated, usually while sitting down. There was ocasionally a mid-morning grazing period followed by a mid-afternoon grazing period. However, there was much day to day variation in grazing time. The sheep seemed to be affected chiefly by heat, and on 15 and 22 July, when temperatures

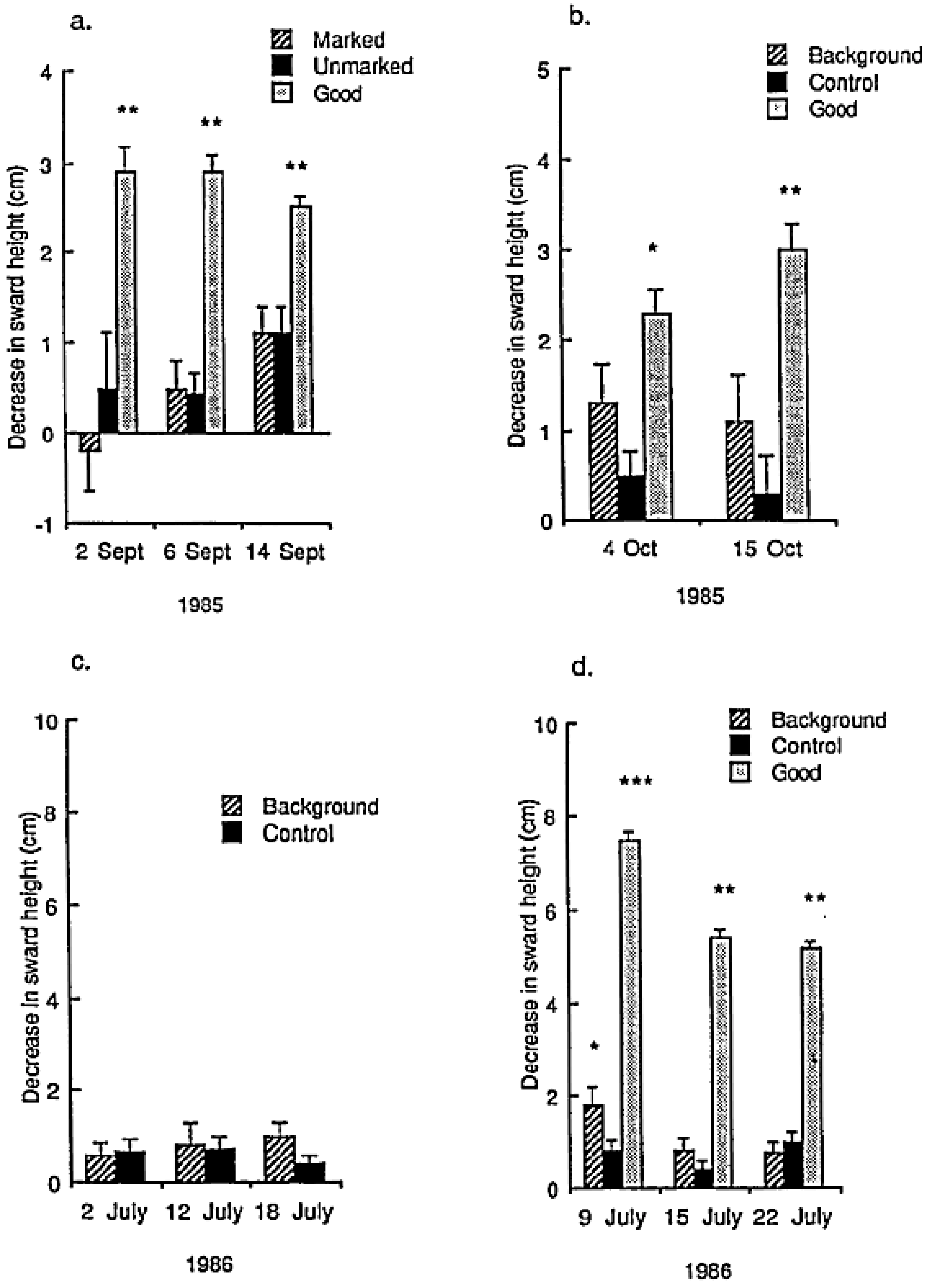

Figure 2.3. Decrease in the initial sward height (cm) of different types of perennial ryegrass swards grazed by sheep on different experimental days.
(a) Experiments in paddock 3, September 1985.
(b) Experiments in paddock 2, October 1985.
(c), (d) Experiments in paddock 1, July 1986.
(Decreases are means; bars are standard errors; ▨ Marked = background sward marked with bamboo poles; ■ Unmarked = background sward without a pole; ⊡ Good = transplanted,

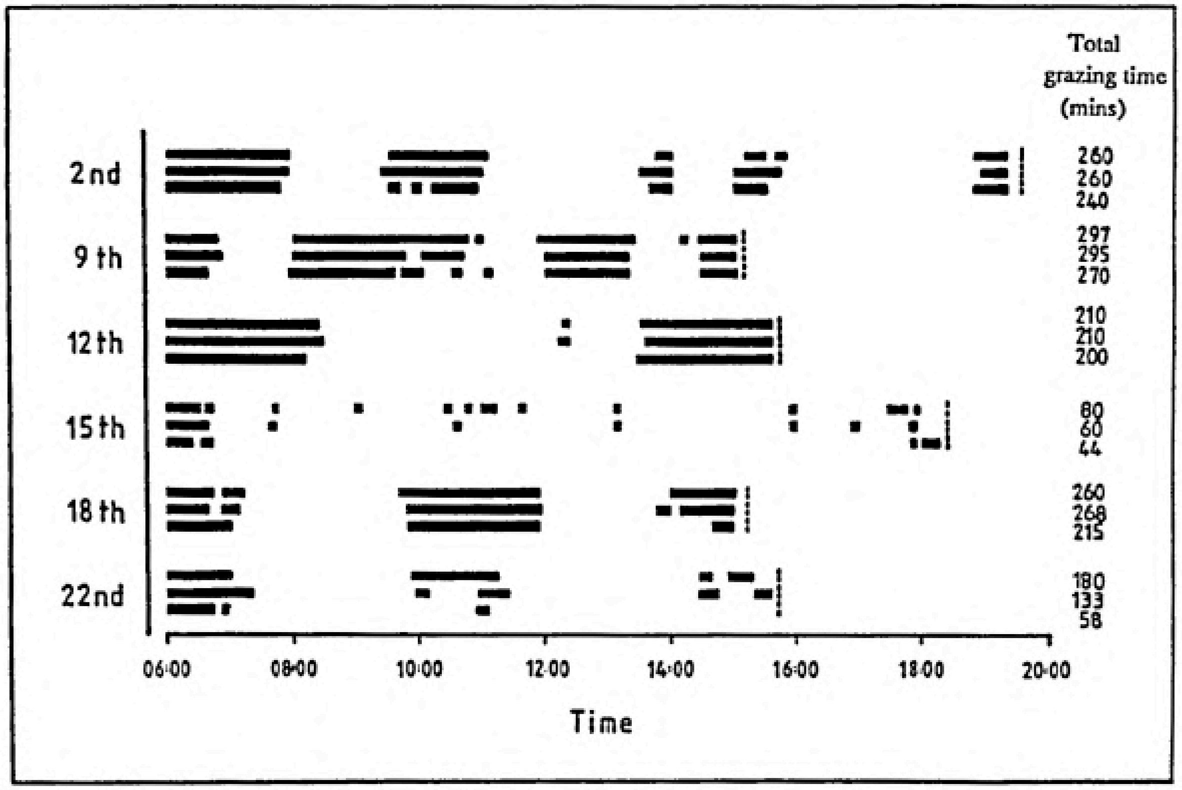

Figure 2.4. Grazing periods of individual sheep on different experimental days in July 1986 indicated by bars. Within each date, the following order denotes specific sheep: top row - sheep 267; middle row - sheep 224; bottom row - sheep 25. Dotted lines mark the end of each experiment.

were in excess of 26°C, sheep 224 grazed for less than one hour, during 10-12 hour experimental periods. The average grazing time per sheep varied from 133-300 minutes on different experimental days except for the 15 July, which was exceptionally warm. The sheep were highly synchronized in their grazing and ruminating behaviour. A similar level of synchrony was observed by Arnold & Dudzinski (1978).

Step and bite rates were calculated from tape-recorded ten minute observation bouts (Table 2.7). Of the two sheep observed, 224 had a greater bite rate than 267 on five out of six days. Bite rates were compared between experiments with and without good patches transplanted into the paddock with a nested ANOVA design for unequal sample sizes. The bite rates were not significantly different between the two treatment groups, in which a treatment was defined by the presence or absence of good patches, for sheep 224 ($F_{s\ 1,31} = 0.90$ n.s.), but there was significant variation among different days within the same treatment group ($F_{s\ 4,31} = 2.74^*$). In the case of sheep 267, bite rates were lower on days when there were no good patches in the paddock ($F_{s\ 1,26} = 5.36^*$), while variation among days within a treatment group (treatment = presence or absence of good patches) was not significant ($F_{s\ 4,26} = 1.25$ n.s.). The lower bite rates were due to sheep 267 spending most of the time grazing tall ryegrass (20 - 25 cm height) along the paddock fence which had escaped mowing. On 2 July 1986, she was observed grazing in the same 8 sq. metre grid square of the paddock next to the fence in 26% of all focal observations collected at 30 second intervals. Bite rates have been found to be negatively correlated with sward height in two other studies in addition to the results presented here (Allden & Whittaker 1970; Penning 1986).

ANOVAs comparing step rates were performed on log-transformed data, to meet homogeneity of variance criteria. In calculating step rates from tape recorded data, three "half-steps" were designated as equal to one full step, because observation indicated that they covered approximately equal distances. Since step rates from all six experimental days for both sheep were very similar, and in one-way ANOVAs on these data no significant differences were found, no further analyses were performed (sheep 224: $F_{5,31} = 1.39$ n.s.; sheep 267: $F_{5,26} = 0.61$ n.s.).

Variation in the movement of sheep was analysed by dividing bouts of steps recorded on tape into two groups: those consisting of three or more consecutive steps which occurred when the sheep moved between "patches" of ryegrass within the sward and those consisting of fewer than three steps, when the animal was feeding within a "patch". "Patchiness" in this context existed purely from the sheep's point of view and the areas between which it may have been moving appeared similar to the human eye. A movement bout was

Table 2.7. Bite and step rates of sheep grazing in paddocks with and without good patches.

		Bites minute^{-1}			Steps minute^{-1}		
		$\bar{X}$	SE	n	$\bar{X}$	SE	n
sheep 224							
No good patches	2 July	19.1	2.9	5	10.6	1.7	5
	12 July	33.5	3.2	6	8.2	0.8	6
	18 July	31.2	3.9	8	6.5	1.0	8
Good patches	9 July	35.8	3.1	8	8.3	1.4	8
	15 July	29.7	6.2	4	19.1	1.1	4
	22 July	34.3	2.4	6	6.5	1.1	6
		Significant variation among days: $p < 0.05$			$F_{5,31} = 1.39$ n.s.		
sheep 267							
No good patches	2 July	11.6	1.6	5	7.7	1.8	5
	12 July	14.6	4.6	5	5.1	1.4	5
	18 July	21.8	7.4	3	4.9	1.2	3
Good patches	9 July	24.1	3.4	8	5.3	1.4	8
	15 July	25.6	2.0	4	8.4	2.1	4
	22 July	19.9	1.8	7	5.2	1.5	7
		Significant variation between patch treatments: $p < 0.05$			$F_{5,26} = 0.61$ n.s.		

defined as each group of movement symbols (full or half steps) bounded by bites. The division of step bout length into two categories was based on two criteria: (1) sheep generally raised their heads and were actively searching for another grazing site when they took three or more consecutive steps; (2) the most rapid change of slope, determined by eye, in log survivor function plots of numbers of steps per bout, occurred at three steps. Thus, the highest proportion of step bouts were two steps or less. The use of log survivor function plots to determine bout lengths is discussed by Slater & Lester (1982).

The total number of movement bouts was determined for each 10 minute observation period, and the proportion of these bouts greater than or equal to three steps in length was plotted against time. The time against which a specific proportion was plotted consisted of the total number of grazing minutes observed prior to the time at which that particular 10 minute period commenced (Figure 2.5). Grazing time for all three sheep was summed to give this total. Thus, after a total of 60 grazing minutes in Figure 2.5, each sheep had grazed on average for 20 minutes. The data were expressed in this form in order to take into account the effect that the sheep had on each other's grazing environment. Data for both sheep for all three days within a particular experimental treatment (paddock with or without patches) were pooled.

Initially, the proportion of movement bouts consisting of three or more steps varied from 30-60% on days with and without patches, and sheep were moving to many different parts of the paddock searching for new grazing sites. By 300 minutes this had dropped to below 20% on days with good patches in the case of both sheep (Figure 2.5b). The type of movement was primarily that associated with intensive grazing, and animals taking one or two steps between bites with their head still down.

On days without good patches, the proportion varied from 20-55% for most of the grazing time and dropped to less than 20% by 600 grazing minutes (Figure 2.5a). These latter points represented observations collected towards the end of experimental days, when the sheep may have been in the paddock for well over six hours. Thus, although the overall step rates (steps min^{-1}) were similar for both treatments, the structure of the movements varied.

This variation was compared between the two treatments in the following analysis. Simple regressions of the proportion of bouts containing ≥ 3 steps per bout against grazing time yielded slopes that did not differ significantly between treatments with and without good patches (comparison of slopes: $z = 0.39$ n.s. df = 1). The slope of both regressions was significantly different from zero ($m_{\text{with patches}} = -0.052^{***}$; $m_{\text{without patches}} = -0.046^{*}$). Regressions were also calculated for all pairs of data points up to, but not

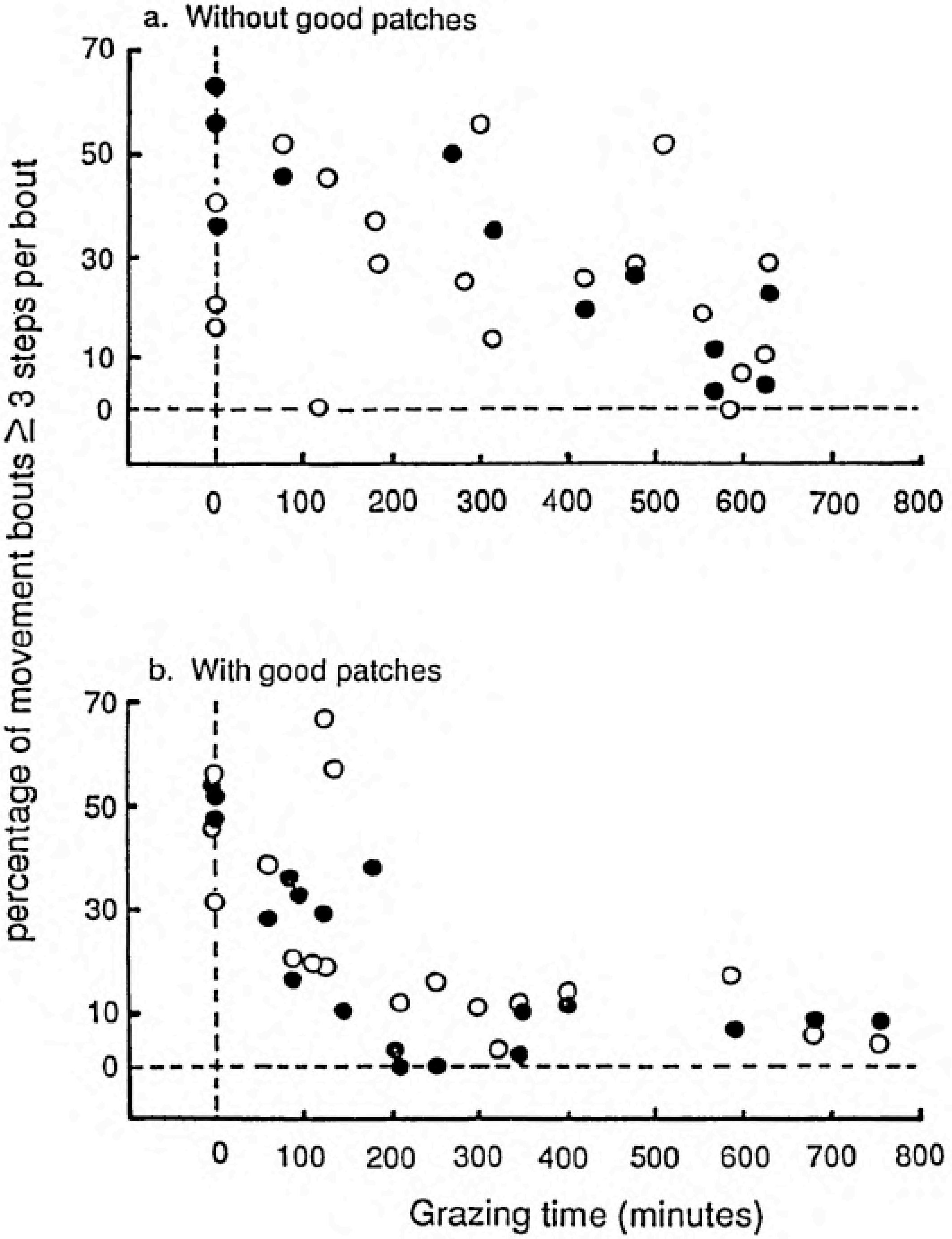

Figure 2.5. Patterns of change in the percentage of movement bouts consisting of 3 or more steps observed during: (a) experimental days without good patches, (b) experimental days with good patches, in July 1986.

(Each point represents a 10 minute observation period; ● sheep 267; ○ sheep 224) including x-values of 300 minutes. On days with good patches, the regression was significant ($y = -0.16x + 47.68$, $F_{1,22} = 18.8^{***}$, $r = 0.68$ df = 22), while on days without patches, the regression was not significant and the slope was not different from zero ($y = -0.01x + 41.10$, $F_{1,11} = 0.12$, $r = 0.10$ df = 11). Therefore, sheep spent a greater amount of their foraging day moving greater distances between consecutively grazed areas of ryegrass on days without good patches.

On days with good patches in 1985 and 1986, the proportion of time spent grazing in good patches was summed for all 15 minute observation periods for each sheep (Table 2.8). Sheep spent 6 - 20% of time grazing in good patches. Mean values from different experimental days carried out in the same paddock were compared with an expected amount of grazing time based on the total area occupied by the patches (0.4% of a paddock). The basis for this comparison was that within a homogeneous ryegrass sward, one might expect sheep to spend equal amounts of time in different areas of the paddock (Crofton 1952). The comparison was based on one-sample t-tests in which the expected population mean of time spent in patches was taken as 0.4%. The observed times were significantly greater in all cases; sheep were selecting the nutritionally good patches, which were structurally reasonably similar to the background sward. On days without good patches, a paddock grid square of approximately 12 sq. metres (2% of the total paddock area) was randomly selected for each sheep. The proportion of observation points in which the sheep were observed grazing in these grid squares was calculated and compared with an expected proportion based on the area of the squares in relation to the whole paddock, using a one-sample t-test (Table 2.9). There was no significant difference.

At the start of experiments, the percentage of bites taken in good patches was high, but this dropped with increased grazing time (Figure 2.6). For both sheep, the linear regression of percent bites on grazing time was significant. Data from three experimental days were pooled for each sheep, and in Figure 2.6, each point represented a 10 minute observation period. Interestingly, not all bites were taken in good patches even early on in the day; the background sward was grazed early on in the experiment. Sheep returned to patches in which they had already grazed, which suggests that even after initial depletion, good patches were still attractive feeding sites, even though they may have been 50% of the height of the background sward. Although linear regressions were similar for both sheep 267 and 224, sheep 267 stopped feeding in good patches sooner than 224.

In summary, all sheep observed spent significantly more time grazing in nutritionally good patches than expected. On days without patches, their grazing time in different paddock grid squares or sectors was

Table 2.8. Proportion of time (observation points) in which sheep grazed in good patches. (Sheep were sampled at 30 second intervals).

Date	Sheep	% time grazing in good patches	total observation period (minutes)	Significance†
1985				
2 Sept	266	16.0	90	
6 Sept	266	6.5	30	
14 Sept	266	8.0	30	
	mean	10.2		t = 5.41*
	SE	2.9		
4 Oct	215	19.5	75	
15 Oct	215	20.0	90	
"	252	18.0	30	
"	267	10.0	45	
	mean	16.9		t = 10.72**
	SE	2.3		
1986				
9 July	224	14.5	90	
"	267	14.5	90	
15 July	224	grazed very little - extremely hot day		
"	267	12.1	60	
22 July	224	grazed very little - extremely hot day		
"	267	26.0	60	
"	266	60.0	17	
	mean	25.4		t = 4.55**
	SE	9.0		

† one sample t-tests comparing mean proportion of time spent grazing in good patches with proportion of paddock area occupied by good patches (0.4%).

Table 2.9. Proportion of time (observation points) in which sheep grazed in a randomly selected grid square in the paddock on days without good patches. (Sheep were sampled at 30 second intervals).

Date	Sheep	% time grazing in grid square	total observation period (minutes)	Significance†
1986				
2 July	224	6.5	75	
"	267	1.5	90	
12 July	224	2.5	60	
"	267	1.7	60	
18 July	224	3.8	90	
"	267	5.2	105	
	mean	3.5		t = 1.75 n.s.
	SE	0.8		

† one sample t-tests compared mean proportion of time spent grazing in grid square with proportion of paddock area occupied by that square (2.1%). Two different grid squares of similar sizes were randomly selected for sheep 224 and 267. The same grid square was used for determinations of grazing time on different days for the same sheep.

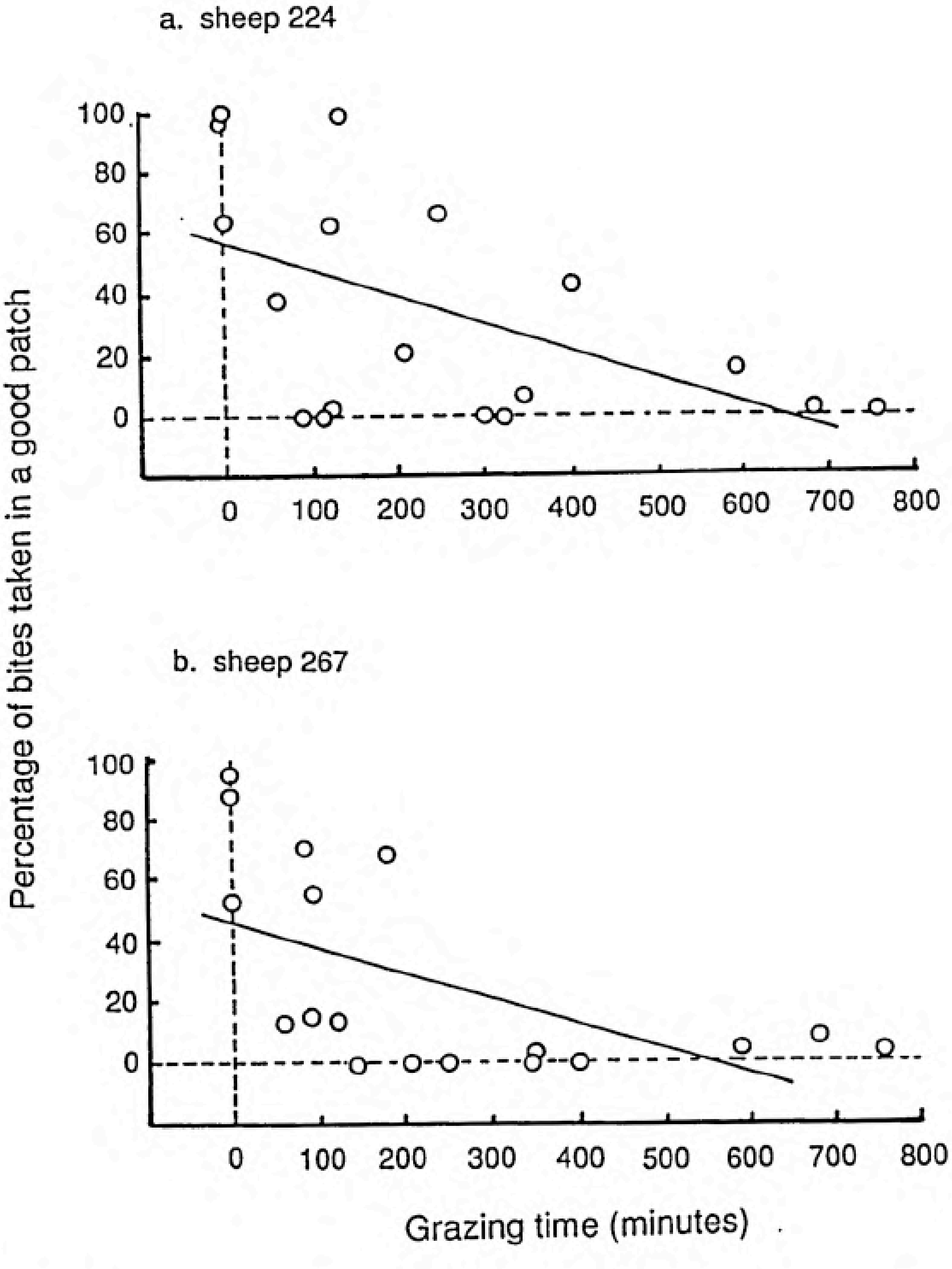

Figure 2.6. Patterns of change in the percentage of bites taken in good transplanted patches during experimental days in July 1986. Lines are simple regressions.

(a) sheep 224. $y = -0.087x + 56.24$, r = 0.53*, df = 16.

(b) sheep 267. $y = -0.084x + 46.07$, r = 0.57**, df = 17.

Individual points represent 10 minute observation periods. Observations were pooled for three experimental days.

proportional to the area occupied by those sectors. However, on some days, sheep 267 grazed tall, unmowed ryegrass along the fence in the same paddock sector for up to 30% of grazing time. Sheep grazed good patches most heavily in the early part of the experiments, although they did return to good patches after they had been depleted. Bite rates of sheep 224 were similar on days with and without good patches, but those of sheep 267 varied because she fed preferentially on much taller ryegrass along the fence on days without good patches. Movement, measured as steps min^{-1}, was similar on days with and without good patches, but the structure of movement varied. A higher proportion of movement bouts throughout the experiment consisted of three or more steps on days without good patches.

2.3 Response of sheep to intra-specific height variation created by transplanting turves into a ryegrass sward

2.3.1 Methods

In section 2.2, the sheep were found to prefer patches of ryegrass which were similar in a variety of structural aspects to the background sward, but higher in nitrogen content and digestibility. However, no information was obtained on whether the sheeps' preferences were influenced in any way by variation in sward structure. Hardison *et al.* (1954) and Black & Kenney (1984) suggested that variation in physical or structural aspects of swards may influence diet preferences. Therefore, the aim of the experiment described in this section was to determine the response of sheep to tall and short patches of ryegrass of similar nutritional quality.

On 21 August 1986, four short and four tall patches were created in paddock 1 by transplanting turves of perennial ryegrass into shallow holes dug in the sward (Figure 2.7). Each patch was 40 cm x 60 cm and consisted of four 20 cm x 35 cm turves held in place with skewers. Turves used were planted in September 1985 with perennial ryegrass seed of a different variety (Parcour) from that in the paddocks (var. Melle). The turves were fertilised twice with approximately 10 g Wiles fertiliser. They had grown to a height of about 15 cm before being used. Prior to transplanting the turves, the sward height of the background sward in paddock 1 was measured with a sward stick (mean = 7.5 cm, n = 54). The transplanted short patches were trimmed to this height, while the tall patches were trimmed to a height of 12.5 cm. The vegetation from three additional replicate turves trimmed to 12.5 cm height was harvested, and divided into two: (1) vegetation from 0-7.5 cm height and (2) 7.5-12.5 cm height. The six samples were washed, dried and analysed for total

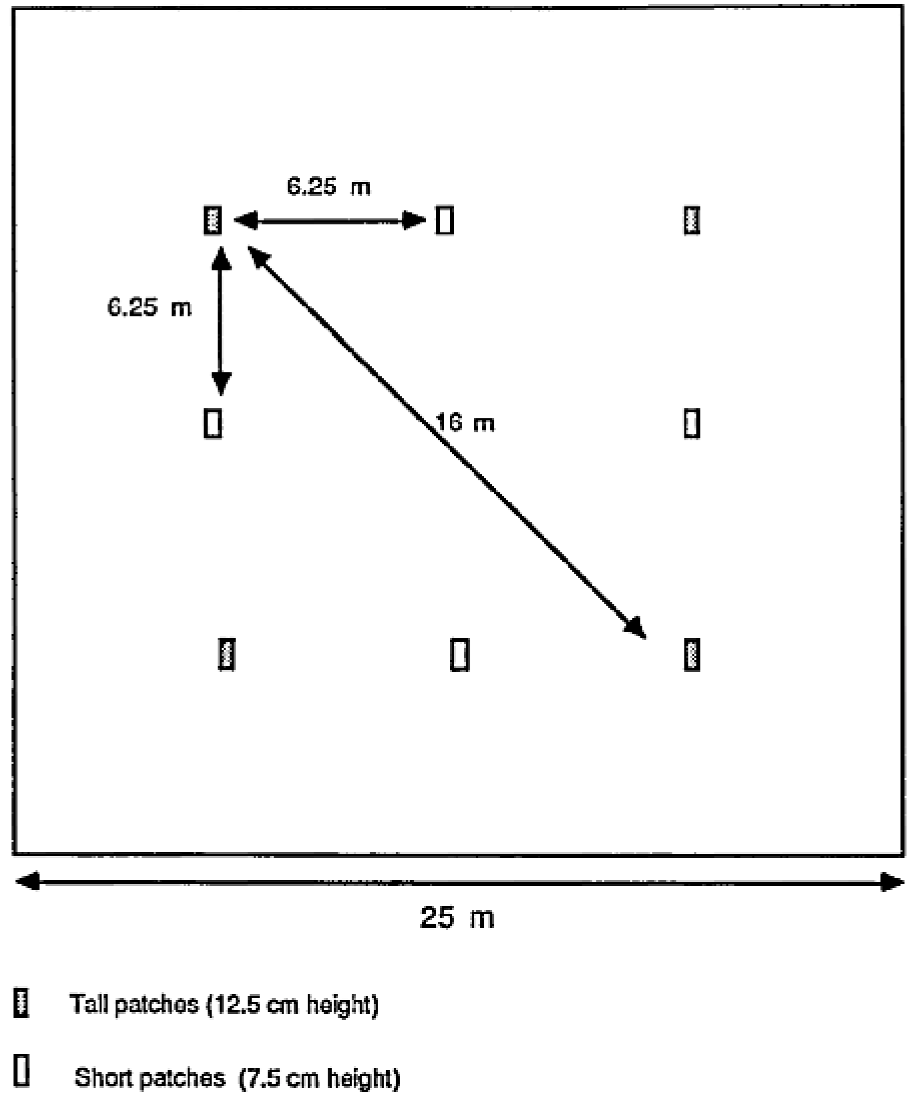

Figure 2.7. Arrangement of transplanted good patches in Paddock 1 for experiment carried out on 22 August 1986.

nitrogen, fibre and water soluble carbohydrate content (Appendix 2.2). The pseudostem lengths of ten ryegrass tillers were measured before samples were cut in half.

In addition to transplanted patches, there were eight patches 40 cm x 70 cm consisting of turves cut from the background sward and rotated at random before being secured with skewers. They were located 2-3 m from the transplanted patches. These were control patches for the effect of sheep being attracted to graze in a particular site by the scent of freshly disturbed earth.

At 08:20 on 22 August 1986, a group of three ewes, numbers 224, 266 and 267, were placed in paddock 1. Sheep 267 was observed in detail for six 10 minute observation periods during which all bites taken were recorded on tape, as well as details of where she grazed. Sward heights were taken in the patches and background sward twice: before the experiment and after it ended at 11:45, when the sheep were removed.

2.3.2 Results

The mean heights of the different groups of patches prior to the start of the experiments were: tall patches 12.9 cm (n = 24), short patches 8.5 cm (n = 24), control patches 7.9 cm (n = 48). The patches were transplanted on the previous day and had grown overnight. At the end of the experiment, when sheep were removed after 3.5 hours, the proportionate decrease in initial height of tall transplanted patches (n = 4) was significantly greater than that of short (n = 4) and control (n = 8) patches (one-way ANOVA: $F_{2,13} =$ 23.9***; Fisher's Protected Least Significant Difference used for multiple comparisons) (Figure 2.8). The ANOVA was performed on angular transformed data. The mean proportionate decrease in height did not differ between short and control patches. It was similar to that of eight points in the background sward selected at random and measured before and after the experiment (n = 6 height measurements per point) also shown in Figure 2.8.

Tall and short patches each covered 0.17% of the total paddock area. Sheep 267 was observed for 70 minutes during the experiment, and 4.5% and 4.1% of bites (n = 2022 total bites observed) were taken in tall and short patches respectively (Figure 2.9). The sheep visited all transplanted patches. The number of bites taken in transplanted patches was significantly greater than would be expected if sheep 267 was grazing them in relation to the proportion of the paddock area that they occupied (Fisher's Exact test $p < 0.001$). The pattern of grazing varied (Figure 2.9), and initially a far higher proportion of observed bites were in transplanted patches. Sheep 267 did not visit these patches from 09:00 - 11:00, but subsequently returned to

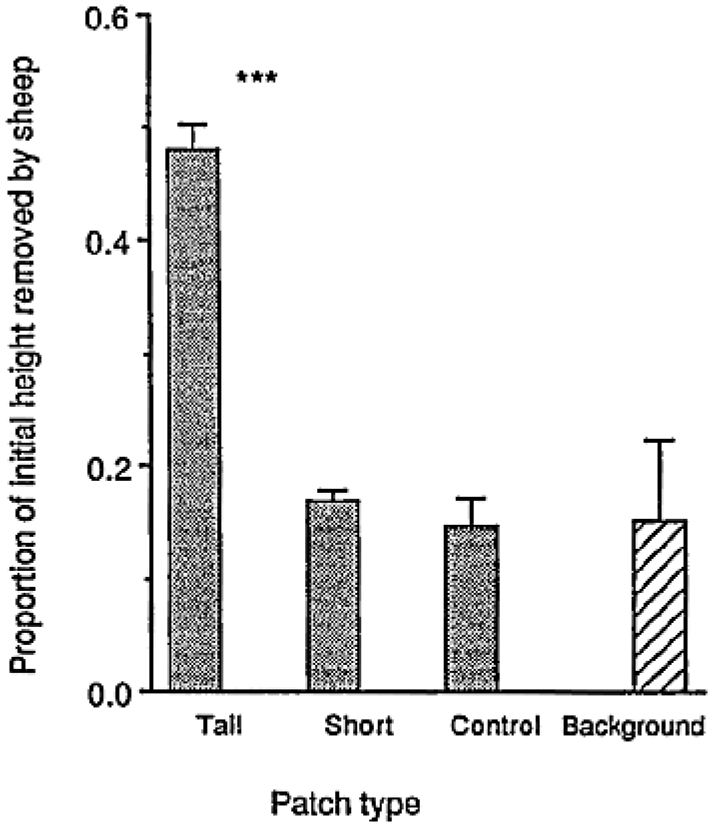

Figure 2.8. Proportionate decreases in the initial sward height of different types of perennial ryegrass swards on 22 August 1986. (Proportions are means; bars are standard errors; n = 4 for tall and short transplanted patches; n = 8 for control patches and unmarked areas of the background sward.)

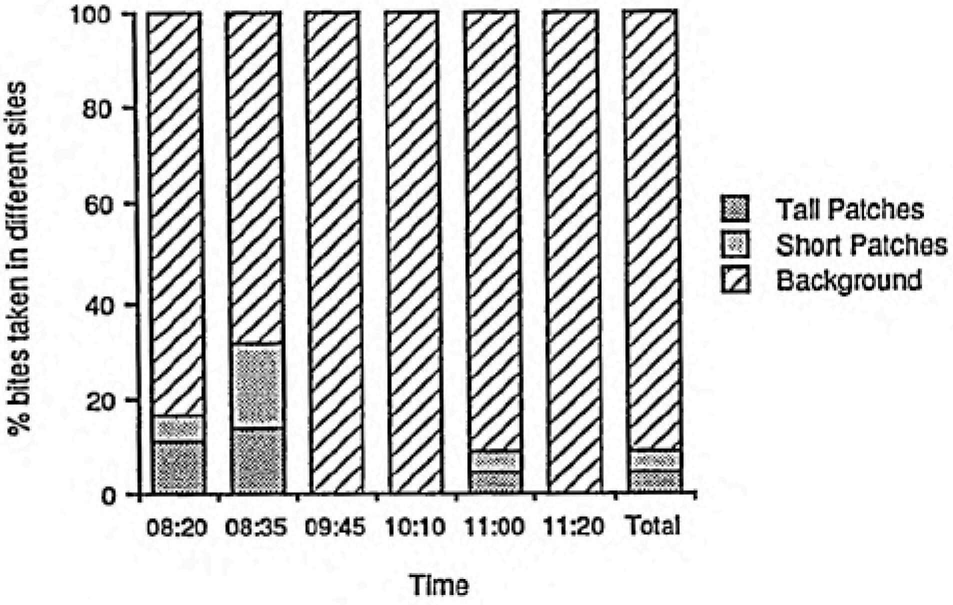

Figure 2.9. Percentages of bites taken at different times of day in different sward types in paddock 1, 22 August 1986, by sheep 267. (The first six bars represent 10 minute observation periods, while the final bar represents observations summed over the 60 minutes.)

them. This pattern was common to all sheep, in that they revisited the same patch more than once during the experiment. Thus the decreases in sward height (Figure 2.8) were gradual and the result of more than one visit.

The mean pseudostem height of transplanted turves was 7.2 cm (S.E. = 2.1, n = 10), which was only slightly less than the height of short patches. The tall patches were grazed to about this height. There was no significant difference between the top and bottom parts of the transplanted turves in nitrogen, fibre and water soluble carbohydrate concentrations (Table 2.10). The chemical characteristics of the turves may be compared with those of the background sward in paddock 1 measured at the end of July 1986 (Table 2.6). The nitrogen content of transplanted turves was significantly greater than that of the background sward.

In summary, the transplanted patches were of higher nutritional quality than the background sward and sheep 267 took as many bites from short transplanted patches as from tall patches. However, the proportionate decrease in height of tall patches was much greater than that of short transplanted patches. This was unexpected, since the same number of bites were taken in both patch types. The small decrease in height may have been caused by the exceptionally long peudostem (7.2 cm) in short patches inhibiting biting depth. Thus, although sheep 267 preferred both tall and short transplanted patches relative to the background sward, her intake from short patches was probably reduced as a result of physical sward characteristics. This effect could not have occurred in the background sward in which the mean pseudostem length in July 1986 was approximately 2.5 cm (Table 2.5).

2.4 Discussion

Sheep spent more time than expected grazing in good patches of perennial ryegrass and also depleted them more than the background sward and control patches, leading to the conclusion that they preferred to feed on ryegrass that was higher in nitrogen content and digestibility than the background sward. Methods of evaluating grazing preferences which have involved measuring time spent grazing in different sites or measuring biomass intake have been commonly used in studies of vertebrate herbivores (Table 2.1), but my experiments differed from previous work in that I attempted to control or selectively manipulate the factors that may influence diet selection. This has seldom been the case in previous studies. As a result, in these studies, alternative explanations may have accounted for sheep selecting diets of higher nutritional content than the overall sward. These explanations were discounted in the present study.

Table 2.10. Chemical characteristics of transplanted turves used for the experiment on 22 August 1986.

Character	Mean	S.E.	n	ANOVA
Total nitrogen (% dry weight)				
0-7.5 cm horizon	3.4	0.05	3	$F_{1,5} = 0.32$ n.s.
7.5-12.5 cm horizon	3.7	0.51	3	
% Fibre (MADF)†				
0-7.5 cm horizon	24.9	0.67	3	$F_{1,5} = 0.06$ n.s.
7.5-12.5 cm horizon	24.3	2.41	3	
Water soluble carbohydrate (mg/g)				
0-7.5 cm horizon	84.5	-	2	$F_{1,4} = 2.55$ n.s.
7.5-12.5 cm horizon	53.4	11.69	3	

†Modified acid-detergent fibre

The "passive" selection hypothesis

Vegetation of varying nutritional quality was available in the upper sward horizon. In addition, the sheep had to travel between nine (or eight) good patches, regularly located throughout the paddock, to obtain the ryegrass of higher nitrogen content or digestibility. Thus, the "passive selection hypothesis", which proposes that sheep select higher quality diets merely by grazing the top layers of vegetation in which the higher quality forage is concentrated, may be discounted in these experiments. Although sheep are better able to reach inaccessible species distributed through the sward (Laidlaw 1983; Grant *et al.* 1985), than are cattle, which tend to remove only the top sward layer (Alder & Minson 1963; Grant *et al.* 1985), the lack of information on the distribution of vegetation of differing nutritional quality through the sward, from earlier studies (Weir & Torell 1959; Arnold 1960b; Arnold 1962; Hamilton *et al.* 1973; Price 1978), has made it difficult to discount this explanation for observed diet selection.

In my experiments it was unlikely that sheep grazed in the locations of good patches purely as a result of their preference for being in a particular part of the paddock. Gibb (pers. comm.) found that sheep preferred to graze near fences and that this preference was unrelated to variation in nutritional quality of the forage. In some trials examining the preferences of sheep and cattle for particular forage species or varieties sown in single strips (Cowlishaw & Alder 1960; Reid *et al.* 1967), results may be influenced by the grazers' preferences for particular sites. However, in most experiments plots sown with different plant species or varieties were usually replicated (Hardison *et al.* 1954; Cowlishaw & Alder 1960).

The control of physical sward parameters

It has long been recognized that total biomass measurements are not the best means of assessing vegetation available to herbivores because not all parts of the sward profile are accessible or nutritionally adequate (Eadie 1970; Black & Kenney 1984). However, variation in biomass may still have an effect on diet choice (Cowlishaw & Alder 1960), although probably through sward height variation with which it is usually correlated (Hodgson *et al.* 1986). Tuenissen *et al.* (1985) speculated that greater biomass as well as higher nitrogen levels attracted Brent geese (*Branta bernicla*) to graze in fertilised sites. Fertilised sites attractive to deer on the Isle of Rhum may also have had greater biomass (Appleby 1980), but neither study recorded whether height was correlated with total biomass. In my inital series of experiments (section 2.2), the total biomass of good patches was significantly lower than that of the background sward in 1986, indicating that sheep preferred to graze in these sites even when there was less biomass present.

Height, and other structural sward parameters that have been found to influence grazing behaviour and therefore possibly diet selection (Hodgson 1982), were controlled in my experiments. However, since the effects of these variables on the mechanics of forage intake, discussed in Chapter 1, have only recently been accurately determined, relatively little is known of their effect on diet preferences of sheep and cattle. Black & Kenney (1984) suggested that sheep may prefer to graze in tall swards rather than short swards. In previous studies of diet selection, sward heights, tiller densities etc. may have been highly variable between different vegetation types (Table 2.1). Data on these parameters were usually not given and apparently not collected, although Cowlishaw & Alder (1960) and Alder & Minson (1963) gave some sward height estimates. In my experiment in section 2.3, while the total overall biomass intake from tall patches was greater than that from short patches, sheep 267 took similar numbers of bites in both types of transplanted patch. Unfortunately I was only able to collect detailed data on one sheep, and I did not know whether other sheep were exhibiting preferences for tall patches reflected by an increased number of bites taken in them. Further experiments on the response of sheep to variation in sward height are described in Chapter 3.

The control and manipulation of physical sward parameters in relation to nutritional quality is acknowledged as being difficult to achieve (Hodgson 1982), but growing turves separately for transplanting was apparently a successful means of by-passing some of the difficulties. Transplantation techniques were successfully used to determine sheep preferences for particular plant species (Lambert 1982) and the effects of goose grazing on survival of plants (Sadul 1987).

The most difficult parameter to control was tiller density which was consistently lower in good patches in the experiments described in section 2.2. At very low tiller densities (<3,000 tillers m^{-2}) herbage becomes increasingly difficult to bite and the rate of intake drops (Black & Kenney 1984). Therefore, it was possible that observed times of sheep grazing in good patches were exaggerated due to lower tiller densities. However, the observed ranges of tiller densities, 5,800 - 10,800 tillers m^{-2} in 1985 and 10,700 - 14,400 tillers m^{-2} in 1986, were well above the level at which prehension slows appreciably.

Although lamina and pseudostem lengths of good patches were sometimes significantly different from those of the background sward, the direction of the differences varied and in biological terms were unlikely to have had an effect on intake since differences were often less than 1 cm (experiments in section 2.2). This was not the case in the experiment on sward height variation (section 2.3), in which pseudostem height appeared to have a marked effect on intake. This illustrates the problem with using only estimates of biomass intake to detect preferences, when structural sward parameters may be influencing total intake. It is important to also collect behavioural data such as numbers of bites taken or time spent grazing in a particular area.

An additional physical factor that was not controlled was toughness of vegetation, characterized as breaking strength. However, if there was a difference between good patches and the background sward in toughness, then one might expect initial bite rates in these sward types to vary. I compared short term bite rates in good patches and the background sward taken from tape recordings from the first 30 minutes of each of the experiments in section 2.2, for sheep 267 and 224, and they were not significantly different. It was not valid to take bite rates from patches later on in experiments, simply because of the confounding effect of decreased sward height on bite rates (Allden & Whittaker 1970; Penning 1986). Interestingly, I did not find differences in bite rates for sheep 267 between tall and short patches. This suggested that the effect of the longer pseudostems in decreasing intake and presumably bite size may have acted through increasing the difficulty of sward penetration rather than increased toughness resulting in a decreased bite rate.

In selecting the size of good patches, I was aware that patchiness exists in grazing environments at a variety of levels. For example, nutritional quality may vary within a single plant and create patchiness on a very small scale. At the next level, patchiness may be created by clumps of different species or by tall areas of vegetation interspersed by short areas. I intended to create nutritional patchiness on the latter scale, for ease of monitoring grazing responses. Bakker *et al.* (1983) studied the development of micro-patterns in plant communities grazed by domestic sheep and found that taller, less heavily grazed areas varied from 0.5 - 3.0 m in diameter. The size of good patches in my experiments, 0.4 x 0.7 m, was based on values from the lower end of this range.

Criteria of nutritional quality

Herbivores must select diets to meet an array of nutritional requirements (Westoby 1974; Stephens & Krebs 1986). Assessing the absolute nutritional quality of vegetation is often extremely difficult because herbivore requirements vary seasonally and different plants may provide different nutrients (Ørskov 1982; Crawley 1983). For example, a particular plant species may provide an essential nutrient such as sodium

(Belovsky 1978) for a herbivore but be low in nitrogen. Therefore, difficulties arise over whether such a species be ranked as high or low quality compared with other diet items high in nitrogen, for example. Nevertheless, the two most important factors affecting survival and reproduction in herbivores are usually considered to be energy intake (Freer 1981; Van Soest 1982), which is related to the digestibility of the diet in ruminants, and nitrogen, particularly for non-ruminants (Mattson 1980; Ørskov 1982). Therefore, the nutritional criteria considered in these experiments were nitrogen, digestibility and also water soluble carbohydrates because they are considered to be the most most important parameters in evaluating forage quality for domestic herbivores (Arnold *et al.* 1966). Also, they are the most commonly analysed biochemical characteristics of vegetation in both the ecological and agricultural literature (Table 2.1).

In the following discussion, I refer only to the results of the chemical analyses presented in section 2.2.2. In 1984, the nitrogen level of background ryegrass was 2.0% and it dropped to below 1.0% in 1985. There was probably an initial effect of residual fertiliser in the soil from previous years. These levels were lower than average for temperate grasslands which range from 0.5 - 5.0% with a mean of approximately 2.2% (Minson 1976 cited in Norton 1982). In 1985, background sward nitrogen levels were below the minimum levels of 0.8-1.5% total nitrogen in forage required for maintenance of rumen microflora populations (Allden 1981; Simpson & Stobbs 1981; Van Soest 1982). Nitrogen levels of good patches were greater than the background sward and varied from 2.5 - 4.0% in 1985 and from 1.0 - 1.5% in 1986. In 1985, nitrogen levels were well within the range found in temperate ryegrass leys, but in 1986 they were lower than average and in the range of threshold values given for minimum requirements for rumen microflora populations.

Digestibility values of the background sward were low to intermediate in comparison with average levels for temperate grasslands which vary from 50 - 80% (Wilson & Minson 1980 cited in Norton 1982). However, they were not as low as those in tropical pastures, which in one study varied from 42 - 75% according to season (Allden 1968). Sheep were unable to maintain their body weight during the dry season, when digestibility dropped to 40 - 50%, even though abundant forage was available (Allden 1968).

In 1985, the range of values for nitrogen content was similar to those given for available and selected forage in other studies (Hardison *et al.* 1954; Weir & Torell 1959; Arnold *et al.* 1966). These studies were often carried out over several months, and estimates of seasonal variation in nitrogen content were available. When mean nitrogen content of vegetation was 2.4%, diets selected were of 2.9% nitrogen content, and when levels in forage increased to 3.2%, the dietary levels of nitrogen increased to 3.7% (Hardison *et al.* 1954). On

Californian rangeland pastures, total nitrogen content in handclipped vegetation samples varied from 1.5 - 3.4% on a seasonal basis while that of fistula samples varied from 2.3 - 4.3% (Weir & Torell 1959). In Australian *Phalaris* -annual grass-clover pastures, the total nitrogen content of forage varied from 2.0 - 4.5% (Arnold *et al.* 1966). However, these studies did not indicate how vegetation varying in nitrogen content was distributed through the sward and whether it was equally available.

In experiments in which plots of different plant species or varieties were sown, animals allowed to visit different plots had more equal access to vegetation of different nutritional value. In a study of sheep preferences for different varieties of Cocksfoot (*Dactylis glomerata*), the nitrogen content of vegetation was greater than that in my experiments, and varied from 3.2 - 3.8% and from 4.7 - 5.0% among varieties depending on time of year (Bland & Dent 1964). However in another study of sheep and cattle preferences for different grass species, values were more similar to those in my experiments, and total nitrogen content varied from 2.5-3.0% in April, and from 1.6-2.8% in June (Cowlishaw & Alder 1960).

It was more difficult to compare digestibility values between this and some of the studies cited above, because they gave raw results from crude fibre analyses. This is a different analytical method from modified acid-detergent fibre analysis. The range of digestibility values measured in my experiments, 68.0 - 77.0%, was similar to that of 65.0 - 82.0% digestibility (%DOMD), depending on season, given by Arnold *et al.* (1966). Digestibility was more variable between good patches and the background sward in my experiments than in Bland & Dent's (1964) study, in which varieties of Cocksfoot grass varied from 77.0 - 77.9% or 75.2 - 77.5% digestibility (% DOMD).

Although background levels of nitrogen were theoretically adequate for the sheep in 1985, their actual requirements may have been greater. Nitrogen demand was observed to increase with digestibility of forage (Ørskov 1982). To maintain rumen functions at optimal conditions on a diet of 70 - 75% digestibility, sheep required the nitrogen content of vegetation to be greater than 2.0%, which would only have been achieved by selecting good patches.

Water soluble carbohydrate values varied from 27.0 - 29.0% in good patches in 1986, and were greater than those given in other studies, which varied from 12.2 - 18.4% at their highest levels in Bland & Dent's study (1964) and peaked at 12.0% in Australian *Phalaris* -annual grass-clover pastures (Arnold *et al.* 1966).

Selection of good patches by sheep appeared to be unrelated to water soluble carbohydrate content of ryegrass, which was both higher and lower than background sward levels on different experimental days. The preferences of sheep for various varieties of Cocksfoot grass were also apparently unrelated to their water soluble carbohydrate content which varied by 6% at most (Bland & Dent 1964). Cowlishaw & Alder (1960) found that preferences of sheep and cattle for different grass species were correlated with water soluble carbohydrate content (combined experiments: $r = 0.51^*$, $df = 6$). However, in their experiment, the animals also had access to plots sown with lucerne (*Medicago sativa*) and clover (*Trifolium pratense*). When I included the water soluble carbohydrate contents and preferences for these additional plots in the correlation, it was no longer significant ($r = 0.41$n.s., $df = 9$). In addition, preference rankings which included only grass species, observed on other occasions by Cowlishaw & Alder (1960), were not significantly correlated with water soluble carbohydrate content.

Grazing behaviour

In the following discussion, I refer only to the behavioural results presented in section 2.2.2. The bite rates of the two sheep observed in 1986 were much lower than those reported in other studies for sheep grazing swards of 8-10 cm height (Black & Kenney 1984; Penning 1986). The mean number of bites min^{-1} varied from 19 - 36 for sheep 224 and from 12 - 26 for sheep 267 on different days. In both other studies, it varied from 50 - 55 bites min^{-1}. My estimates of bite rates were based on ten minute periods and included time taken to move between different parts of the sward being grazed. I assumed that if there was any difference in biting behaviour between experimental days with and without good patches, it would arise from differences in time spent moving around the paddocks while sheep were grazing, and that this would be reflected in variation in bite rates when they were measured over longer periods. Black & Kenney (1984) estimated rates over short time periods which included only grazing time, which may explain why their values were greater. Penning *et al.* (1984) and Penning (1986) measured bite rates over 25 - 200 minute periods with automatic recording equipment. Although they found that manual observations of bite rates were significantly lower than automatically recorded observations, this difference amounted to only 10 bites min^{-1}. However, the sheep observed in their tests had not recently been introduced to paddocks, as was the case in my experiments, and it was possible that their sheep spent less time walking around.

The bite rates observed for both sheep on 2 July 1986, when there were no good patches, were 10 - 14 bites min^{-1} lower than on days with good patches and were explained by sheep grazing much taller grass along the paddock fence. Penning (1986) found that bite rates declined by approximately 17 bites min^{-1} for sheep grazing 12 cm high swards compared with 9 cm high swards, which was a comparable decrease of bite rate with increased sward height.

Sheep 267 had a much lower bite rate than 224, even on days with good patches, when she did not graze tall grass along the paddock fence. In indoor trials described in Chapter 4, sheep 267 was again found to have consistently lower bite rates when compared with four other sheep. This suggested that variation in bite rates between individuals was fixed to some extent. Neither Black & Kenney (1984) nor Penning (1986) gave information on individual variation in bite rates. It is interesting to speculate whether there is a heritable component to bite rate, particularly since it is a factor directly related to total intake (Illius & Gordon,1986).

The means by which the sheep detected the good patches may have involved the use of senses of taste, smell, touch, and sight. The good patches were distinguishable from the background sward chiefly by their different brightness, although they may also have smelled different. In Chapter 3, the relative importance of these mechanisms is discussed in more detail along with results of experiments investigating the response of sheep to variation in the visual appearance of swards which followed on from the section 2.3 experiment. Learning mechanisms which may account for sheep associating patches of a particular brightness with a particular nutritional quality are also discussed.

One reason why sheep found the good patches in the paddocks, was that at the start of all experiments, they moved around the paddocks a great deal, as indicated by the proportion of movement bouts greater than two consecutive steps. Westoby (1974) has discussed the importance of vegetation sampling for herbivores, but few data on this type of behaviour are available. The greater amount of movement by sheep at the start of experiments may be explained in terms of their need to sample and explore their new environment. As experiments progressed, the proportion of step bouts greater than two consecutive steps in length declined, and sheep grazed more intensively, and looked around less for new grazing sites.

The reason why the structure of movement bouts measured as the number of steps per bout, differed between days with and without good patches is unclear (section 2.2.2). I had not expected to find an observable difference, but if I had, I would have predicted the opposite: that after some initial sampling or exploration, sheep in a homogeneous ryegrass paddock without good patches would move around primarily in bouts of less than three consecutive steps. Presumably the sheep would learn that the paddock was homogeneous and would therefore maximize intake by grazing intensively between half or single steps. However, this was not the case, and they continued to take more bouts of three or more steps as experiments went on, compared with days with good patches. There are two possible explanations for these observations. Firstly, that sheep remembered from previous days and the previous year that there had been good patches and continued to move around the paddock throughout each experiment, searching for them. Secondly, if long step bouts are interpreted as characterizing more selective grazing, as opposed to "lawn-mower" like grazing, then in a low nitrogen sward the sheep may have needed to maintain highly selective behaviour for longer periods than on days when good patches were available. An observation that supports the latter interpretation of the maintenance of selectivity was that sheep grazed the flower heads of taller, unmowed ryegrass along the paddock fence only on days without good patches. This interpretation requires sheep to be able to assess and respond to changes in their physiological requirements on a short term basis of a few hours.

Are domestic ruminants comparable to wild herbivores?

Two questions are raised when one attempts to place results from studies of diet selection in domestic ruminants in a wider context, as has been done in Table 2.1:

1. How comparable are ruminants and non-ruminants?
2. How valid are comparisons between wild and domestic herbivore populations?

Domestic sheep are ruminants, which are a suborder, the Ruminantia, of the Artiodactyla, the ungulates (Van Soest 1982). Most herbivores can only utilize soluble components of plant cells in their diets (Van Soest 1982). However, as a result of their distinctive digestive morphology, ruminants are able to take advantage of plant cell wall constituents in their diets. Their rumens contain bacteria which breakdown cellulose under anaerobic condititions, and the by-products of this fermentation are available as energy sources to the herbivore host (Van Soest 1982). While there may well be some justification for the opinion that relative to other vertebrate herbivores, ruminants are particularly well adapted to feed on low quality vegetation (Ørskov 1982 ; Van Soest 1982), it would be incorrect to conclude that they can afford to be unselective in their feeding behaviour. Much vegetation is of unacceptable nutritional quality for wild African ungulate populations (Sinclair 1975). Price (1978) found that without selective grazing of available vegetation, Coke's Hartebeest (*Alcelaphus buselaphus cokei*) were unable to meet their basic maintenance requirements.

The second question is of interest in this study, because one might ask how observed grazing behaviour and diet selection in sheep contributes to an understanding of the behaviour of wild ruminants. This question has been debated most recently in a discussion of whether the evolution of flocking and herding behaviour was related to food yield from grazing sites as well as to protection from predators (McNaughton 1984, 1986; Westoby 1985, 1986).

It is unlikely that artificial selection has resulted in the absolute "breeding out" of behavioural traits related to diet quality discrimination in sheep. In many studies of cattle and sheep, the selected diets were nutritionally better than available forage, which was also the case in my experiments. Many domestic herbivore populations live on rangelands and uplands in semi-feral conditions and must graze selectively in order to meet their basic nutritional requirements (Weir & Torell 1959; Eadie 1970; Allden 1981). Dominance hierarchies are maintained in groups of domestic sheep and cattle (Rutter *et al.* 1987; Lawrence & Wood-Gush 1988), as are feeding behaviours similar to those observed in Red deer populations in which subordinate stags were displaced from forage by dominant individuals (Appleby 1980). Lawrence & Wood-Gush (1988) observed that older, dominant Scottish Blackface ewes actively prevented younger subordinates from gaining access to feed-blocks distributed on hillsides in the winter. In my experiments, it was often the case that the dominant sheep in the trio displaced the other two from good patches.

An additional selection pressure that has often been postulated as being important in the evolution of ruminants is predation (Van Soest 1982). Although the percentage of energy invested by domestic animals in predation avoidance will be different from that of wild animals (Broom 1981), domestic sheep still exhibit anti-predator behaviours such as flocking. While total grazing time available is greater for domestic herbivores, it is difficult to predict exactly how diet selection in sheep will have been affected. One possible hypothesis is that domestic herbivores should be even more selective than their wild counterparts because they have been artificially selected for rapid growth and one factor which may influence this parameter is increased diet selectivity. Digestive efficiency is one physiological characteristic that removal of predation pressure has not changed. Digestive efficiencies measured across a range of species were found to be similar for both wild and domestic ruminants (Price 1978)

Thus, there are many similarities in behaviour and physiology of wild and domestic ruminants. The great advantage of domestic herbivores is that controlled grazing experiments can be carried out more easily.

Extrapolating selection in monocultures to multi-species plant communities

As discussed in Chapter 1, in multi-species plant communities many factors other than nutritional content of vegetation, characterized by total nitrogen, digestibility etc., influence diet selection. When herbivore preferences for different plant species cannot be explained on the basis of regular nutritional parameters (e.g. Warmke *et al.* 1952) they are likely to be related to the presence of other unknown compounds. Because of this, it is arguable as to whether it is worthwhile attempting to interpret diet preferences in multi-species plant communities on a strictly nutritional basis, even when all available species are known to be acceptable and non-toxic. It is more profitable to evaluate the ability of herbivores to select vegetation on the basis of its nutritional content on an intra-specific basis, as was the case in the experiments presented in this chapter, since the presence of different secondary compounds is less likely to be important in influencing selection. However, in studies such as this, it is important to ensure that there is a wide enough range of nutritional values to enable animals to be selective (Eadie 1970). This may not have been the case in Bland & Dent's (1964) study which examined sheep preferences for varieties of Cocksfoot. In addition, it is important to bear in mind that in some situations where a particular nutrient is not limiting and well above requirements, selection for it may not be observed (Arnold *et al.* 1966).

Chapter 3

Responses of sheep to variation in two components of the visual aspect of perennial ryegrass swards: height and brightness

3.1 Introduction

In Chapter 2 experiments, I was primarily concerned with investigating the grazing behaviour of sheep feeding on perennial ryegrass, in which structural sward parameters were held constant, while biochemical parameters were manipulated. Structural sward parameters which may influence grazing behaviour are height, tiller density, and pseudostem and lamina length (Hodgson 1982; Black & Kenney 1984). In addition, a second, brief experiment, described in section 2.3, investigated the behaviour of sheep grazing in swards in which some of these structural parameters were varied. The field experiments described in this chapter were based upon and extended those described in Chapter 2, particularly the second experiment.

Variation in sward height within a ryegrass pasture is, above all, variation in a property of its visual appearance. The brightness, or "shade" of green, is an additional visual characteristic of swards which may vary greatly. I observed two sources of variation in the brightness of ryegrass swards: (1) within the nutrient deficient ryegrass paddocks, there were darker green patches in the vicinity of sites where sheep had provided a nutrient input via urination or defaecation; (2) in the experiments described in Chapter 2, the transplanted patches, which were fertilised, were darker green than the background sward. From a human perspective, the main difference between the transplanted turves and the background sward in experiments in section 2.2, was in their visual appearance, although they may also have had a different odour which sheep were able to detect. Therefore, a possible mechanism used by sheep to locate transplanted patches of similar height to the background sward, may have been their relative brightness.

Although the colour or brightness of ryegrass may be regarded as a physical characteristic of the sward, it was not considered, along with structural or morphological sward parameters, as possibly influencing grazing behaviour, in any of a number of reviews of the subject (e.g. Arnold & Dudzinski 1978; Arnold 1981; Hodgson 1982). Thus, while structural sward parameters were controlled or manipulated in the first set of experiments described in Chapter 2, the brightness was not considered. The overall aim of the experiments described in this chapter was to investigate further the response of sheep to manipulations of the visual appearance of perennial ryegrass swards. I focused on two physical sward parameters: height and brightness. Specific hypotheses relating to expected behavioural responses of sheep, as well as the possible role of vision in these responses, are discussed in the sections below. These field experiments differed from those described in Chapter 2, in that within-sward variation in height and brightness was not created by transplanting turves, but by *in situ* sward manipulations. Also, differences among heights of different areas of the sward were much greater than 5cm.

The role of vision in grazing

From his experiments investigating the role of vision in diet selection in sheep, Arnold (1966a) concluded that sight was not particularly important, and that its main function was to orient the animal to its environment. In most of his experiments, the diets selected by blindfolded animals were not significantly different in species composition or nutritional quality from those selected by animals without blindfolds. Unfortunately, it was often the case that sheep did not become accustomed to the blindfolds, and grazed for short periods, thereby resulting in relatively few data being collected (Arnold 1966a).

In reviews of sheep grazing behaviour, these experiments are frequently cited as demonstrating the lack of importance of vision in diet selection (e.g. Arnold & Dudzinski 1978; Arnold 1981). However, other herbivores, specifically, the frugivorous monkey, *Callicebus torquatus*, is thought to locate food by using primarily visual cues, and to respond to both variation in colour and brightness of fruit (Snodderly 1979). Sheep have binocular vision (Whitteridge 1978) and are able to discriminate detail on a fine enough level to distinguish between the faces of familiar and unfamiliar conspecifics (Kendrick & Baldwin 1987). They appear to use sight to distinguish between white clover polymorphisms, and preferentially select leaves without white leaf marks (Cahn & Harper 1976). Other ungulates such as Pygmy goats (*Capra hircus* L.) and Red deer are able to discriminate fine detail in patterns even under relatively dim light conditions (von Backhaus 1959).

Arnold (1966a) described some experimental results in which blindfolded sheep grazing in monocultures selected less nutritious diets. Despite these results, he drew the conclusion about the importance of vision in diet selection described above. Therefore, a re-examination of its role in diet selection in sheep seemed pertinent in a study of grazing behaviour.

Sward height

Sheep may be expected to respond to variation in sward height because height is positively correlated with bite size (Black & Kenney 1984). Thus, the selection of taller swards would be a means of increasing intake rate. This would result in a decrease in foraging time, if nutritional requirements were met within a shorter period and animals were not limited by digestive constraints. In field trials, total daily grazing time was observed to be less for sheep grazing taller swards than for animals on shorter swards (Allden & Whittaker 1970), although the animals were unable to choose the sward in which they grazed. Interestingly, in Chapter 2 (section 2.3), while the total intake from tall patches of ryegrass was greater than that from short patches, sheep 267 took similar numbers of bites from both types of patches, suggesting that her preference for both patch types was similar.

The hypothesis that sheep should select taller areas of ryegrass in which to graze (Black & Kenney 1984), runs counter to observations of grazing behaviour, and a general consensus that sheep and cattle prefer to graze in shorter vegetation (Arnold 1964, 1966b; Van Soest 1982). Cattle may avoid taller patches of vegetation, but usually because they have been contaminated through urination and defaecation (Plice 1951). Sheep grazing in multi-species plant communities often prefer to graze in shorter areas of vegetation and avoid taller, rank areas dominated by unpalatable species (Bakker *et al.* 1983; Grant *et al.* 1985. D. R. Bazely unpubl. data). However, to my knowledge there are no published studies in which preferences have been assessed for herbivores offered a choice between vegetation or grass swards of different heights, both of which are uncontaminated and of similar nutritional quality.

Sward brightness

The term "luminance" refers to the total amount of incoming radiation reflected from an object (Jacobs 1981) and I use the term "brightness" to have the same meaning. Brightness is a quantity unrelated to "hue" or "colour", which refer to specific wavelength characteristics of an object. Responses of sheep to variation in hue or colour of grass was not considered in these experiments, since sheep do not have colour vision (Tribe & Gordon 1949 cited in Jacobs 1981).

In field observations, transplanted, fertilised ryegrass patches were darker green than unfertilised swards. Thus, the brightness of ryegrass appeared to be related to its nutritional content, and sheep may have learned to use this as a cue to graze in good patches. Therefore, one hypothesis considered in this chapter was that sheep should prefer to feed on darker green ryegrass. In addition, the quantitative relationship between brightness and nutritional quality of ryegrass was investigated.

Height and brightness

I observed that height and brightness were often positively correlated in paddocks allowed to grow up after mowing. Therefore, in some experiments, I attempted to vary these two parameters independently. It was not possible to carry out a factorial experiment to evaluate the responses of sheep to all combinations of height and brightness (tall + light green ryegrass, tall + dark green ryegrass, short + light green ryegrass, short + dark green ryegrass) due to lack of time. Although I manipulated visual parameters of ryegrass, I was unable to control for variation in odours. Thus, it was possible that visually manipulated ryegrass also varied in its odour and that sheep might have been responding to olfactory cues. However, experimental results suggest that the sense of smell does not influence preferences of sheep for different varieties of clover (Tribe 1949) or perennial ryegrass (Arnold 1966b). Animals with an impaired sense of smell preferred similar varieties to those with intact senses. Therefore, I assumed that smell was not greatly influencing intra-specific choice. The experiments described in this chapter are summarized in Table 3.1.

3.2 Response of sheep to variation in height and brightness in a perennial ryegrass sward created by *in situ* manipulations of swards

Methods

Four 25 m x 25 m paddocks sown with perennial ryegrass (var. Melle) in April 1985 were used. They had been fertilised and their grazing history in 1985 was described in chapter 2.

Throughout this section the description of ryegrass as dark green or light green refers to the "brightness" or amount of light reflected by the sward. Thus, dark green grass reflected less light than light green grass. Methods of quantifying brightness are described in section 3.3. The differences in brightness of ryegrass described in this section (3.2) in a qualitative sense, were checked against measurements made on colour slides of the relevant swards using a transmission densitometer.

3.2.1 Experiment 1: Response of sheep to naturally created variation in intra-specific height and brightness

3.2.1.1 Methods

In experiment 1, my aim was to determine whether the grazing preferences of sheep were influenced by variation in the physical structure i.e. height, within a monoculture of perennial ryegrass. In section 2.3,

Table 3.1. Summary of experiments presented in Chapter 3.

Section	Experiment number	Relationship or behavioural response investigated
3.2	1	Response of sheep to tall, naturally created (*in situ*) patches of ryegrass in which brightness and height were correlated.
	2	Response of sheep to tall dark green patches and short dark green patches of ryegrass (all patches were the same variety of ryegrass relative to the background sward).
	3	Response of sheep to tall light green patches and short dark green patches of ryegrass (all patches were the same variety of ryegrass relative to the background sward).
3.3	-	Relationship between brightness of ryegrass and its nutritional quality.
3.4	-	Preference of sheep for dark green or light green trays of ryegrass.

sheep 267 took as many bites in tall as in short transplanted patches. Therefore, from this perspective, there was no clear preference shown, although the proportionate intake from tall patches was greater. Therefore, the role of height was investigated futher, with tall patches, which were also darker green than the background sward, created by allowing paddocks to grow up after mowing.

Variation in sward height was created by allowing a grazed and then mowed 25 m x 25 m paddock to grow for 4-6 weeks. Ryegrass in the vicinity of sites where grazing sheep had urinated or defaecated grew up, after mowing, to be much taller than the background sward.

In 1986 paddock 2 was prepared in this way and in 1987, paddocks 2 and 3 were used. The number of identifiable tall patches in each paddock was counted, and in 1986 five of these patches were selected at random and marked with bamboo sticks hammered into the ground 1 m away. Five sward height measurements were taken in each patch (see chapter 2.2). Five sward heights were taken in shorter grass 50 cm from the edge of the patch. Five additional sites were selected at random throughout the paddock in the short sward and at each of them five height measurements were taken in a circular area of 80 cm diameter. This was the approximate diameter of the tall patches. I wanted to compare the height of shorter swards near tall patches with that of shorter swards further away from these patches, in order to demonstrate the highly localized effect of nutrient input from faeces and urine. Beyond the much taller, dark green patches, there may have been a diminished, but additional effect on sward height caused by the outward leaching of nutrients, rather than an abrupt decline in the effect.

On 27 August 1986, a group of three ewes (numbers 212, 220 and 248) was placed in paddock 2 at 16:15. The sheep were observed for two 15 minute periods, separated by a period of five minutes. At 15 second intervals, each sheep was scored as to whether it was grazing in a tall patch. After one hour the experiment was terminated and the heights of the marked patches were measured. In addition, the number of identifiable tall patches that had been grazed was scored.

In 1987 the same procedure was followed, but ten tall patches in each paddock were marked and ten points were selected at random for measurement in the short background sward. The sample size was increased because there were more tall patches in paddocks and so perhaps a decrease in the likelihood of all patches being visited by sheep.

On 27 June 1987, sheep 23, 180 and 211 were placed in paddock 3 at 13:30 hours. They were observed for two 15 minute periods and at 15 second intervals each sheep was scored for its behaviour in the following three categories: (1) grazing in a tall patch, (2) grazing in the shorter background sward, (3) other activities, such as walking or standing. After two hours, the experiment was terminated and the sheep removed from the paddock. Following their removal, the heights of the ten marked tall patches and the short sward on their periphery were measured and tall patches were scored for whether they had been grazed.

On 28 June 1987, sheep 25, 88 and 107 were placed in paddock 2 at 12:35. The same procedure was followed as on the previous day, except that there were three 15 minute observation periods because the sheep ruminated less, thereby allowing the collection of additional data.

3.2.1.2 Results

The mean heights of naturally created, tall ryegrass patches were 9-13 cm greater than the background sward 50 cm away and elsewhere in the paddocks (Table 3.2). These differences were significant when compared with the Minimum Significant Differences (MSD) calculated by the Studentized range procedure (T-method of Sokal & Rohlf 1981), for unplanned *(a posteriori)* comparisons. For these comparisons, sward height measurements were pooled among different sites of the same sward type.

In all experiments, all marked tall patches were intensively grazed by sheep and their heights decreased by 30-40% (5 - 8 cm) compared with 1-10% (0.2 - 1.0 cm) in the short sward 50 cm away (Figure 3.1). The mean initial height of each patch or adjacent short sward was subtracted from its mean final height and this difference expressed as a proportion of the initial height: n = 5 tall/ adjacent short sward sites in 1986 and n = 10 patches per paddock in 1987. Height decreases were significantly greater in tall patches (one-way ANOVA: 27 Aug 1986 $F_{1,9} = 26.5^{***}$, 27 June 1987 $F_{1,19} = 26.5^{***}$, 28 June 1987 $F_{1,19} = 28.4^{***}$). Proportion data were transformed with the angular transformation, arcsin $\sqrt{(\text{proportion})}$, where required (Rohlf & Sokal 1981, Table 5).

In 1986, sheep spent 33-48% of 30 minute observation periods grazing in tall patches (Figure 3.2a). They were sampled at 15 second intervals. In 1987, the amount of grazing time was separated from time spent in other activities, and results are presented as the percentage of grazing time (15 second spot observations) spent feeding in tall or short swards (Figures 3.2b,c). Sheep spent from 50 - >90% of grazing time feeding in tall patches. When time spent grazing in tall patches was calculated as a proportion of total observation time, it varied from 60-85% in paddock 2 and 27-70% in paddock 3 (n = 45 and 30 minutes total observation time respectively).

Table 3.2. Heights of different types of swards in paddocks sown with perennial ryegrass after the paddocks had grown for 4-6 weeks following mowing and before they were grazed by sheep. The paddocks contained easily identifiable tall patches.

Date	Type of sward	$\overline{X}$ height (cm)	Standard Error	n	one-way ANOVA for different sward types
27 Aug 1986	Tall patches	21.5*	0.60	25	
	Short, close to tall patch	11.8	0.47	25	$F_{2,74} = 128$*** M.S.D.[†] = 1.83
	Short, selected at random	10.2	0.54	25	
27 June 1987	Tall	15.1*	0.58	60	
	Short, close to tall patch	6.5	0.18	60	$F_{2,179} = 171$*** M.S.D. = 1.26
	Short, selected at random	6.6	0.24	60	
28 June 1987	Tall	20.9*	0.36	60	
	Short, close to tall patch	8.2	0.24	60	$F_{2,179} = 720$*** M.S.D. = 0.94
	Short, selected at random	7.6	0.21	60	

[†] Studentized range Minimum Significant Difference at $p = 0.05$.

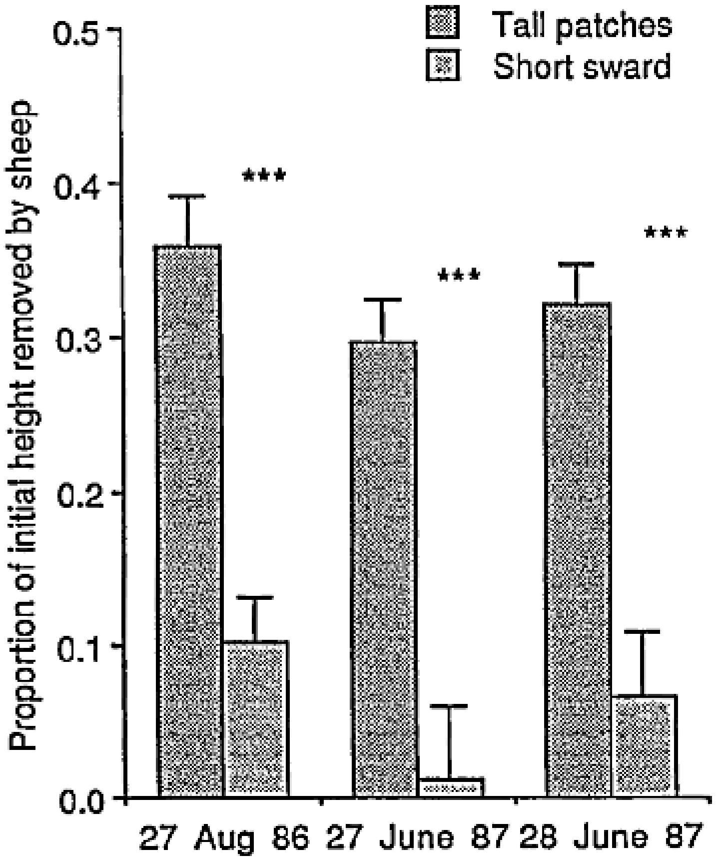

Figure 3.1. Proportionate decreases in the initial sward heights of tall patches (▨) and areas in the background sward (▨) of perennial ryegrass paddocks on different experimental days.

(Proportions are means; bars are standard errors; n = 5 in 1986; n = 10 in 1987.)

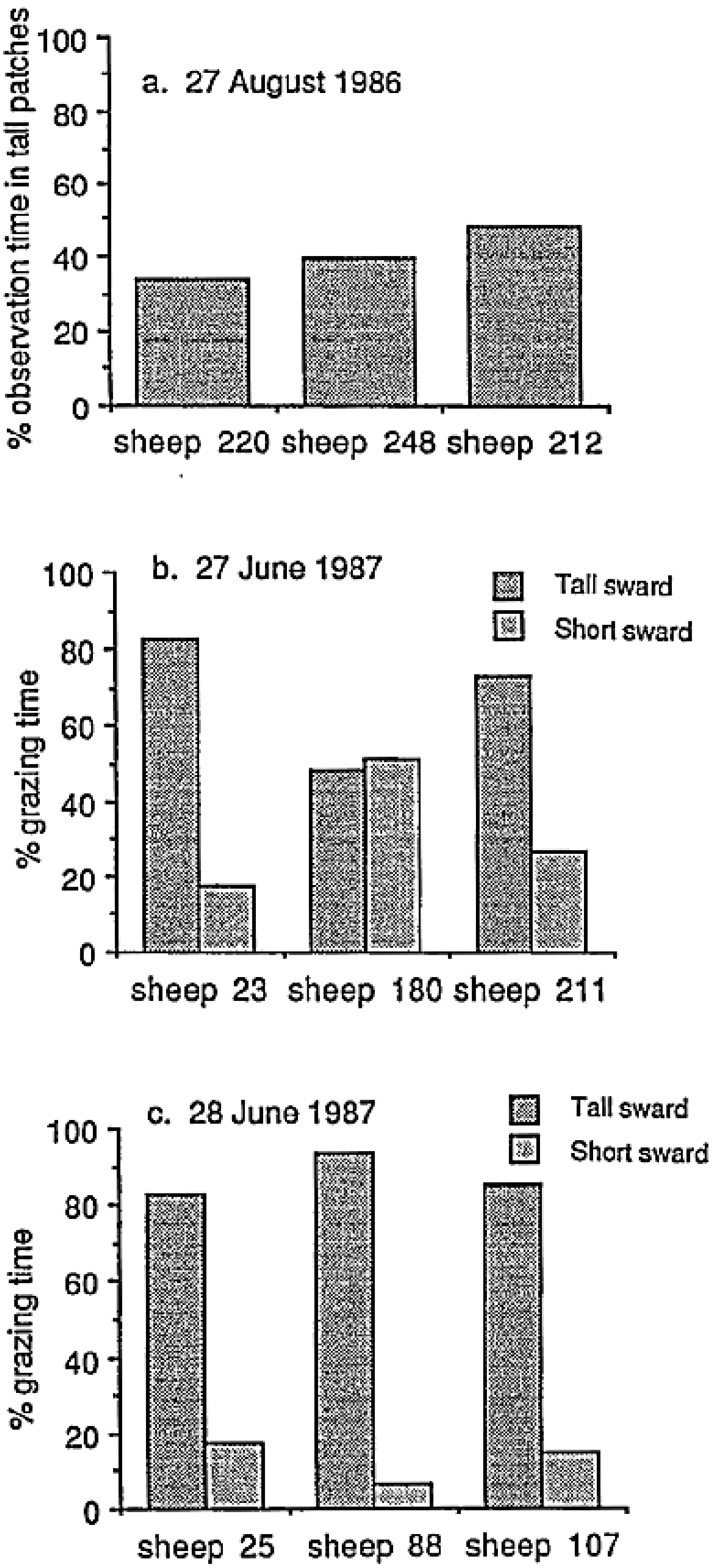

Figure 3.2. Percentage of time spent grazing by sheep in tall patches (sward) (▨) and shorter background sward (▨) of perennial ryegrass on different experimental days.

(a) 27 August 1986 (30 minute total observation period).

(b) 27 June 1987 (30 minute total observation period).

(c) 28 June 1987 (45 minute total observation period).

Tall patches constituted 4 - 7% of the total paddock areas (Table 3.3) and an expected number of observation points for sheep grazing in tall patches and shorter background sward was calculated for each paddock based on these percentages. Since observation points collected at 15 second intervals may have been interdependent, three out of four consecutive points were dropped from the analysis. The average time spent grazing in a tall patch was 15 - 30 seconds, and a sheep could walk from one side of the paddock to the other in less than 30 seconds, so it was assumed that sample points taken at one minute intervals would be independent. Therefore, observed and expected values of where sheep were/should be grazing were based on a reduced number of points and they were compared using Fisher's Exact tests. In both 1986 and 1987, all sheep spent significantly more time (observation points sampled at one minute intervals) grazing in tall patches than would have been expected if grazing time was dependant only on the area of the paddocks occupied by these patches (sheep 220: $p = 0.011$; sheep 212: $p = 0.003$; other seven sheep $p < 0.001$)

After 1-2 hours, 70-80% of identifiable tall patches were grazed, which was another indication that sheep were particularly attracted to graze in them.

In summary, sheep in all experiments preferred tall, naturally created dark green patches, and spent significantly more time than expected grazing in them. This was reflected in the greater proportionate decrease in height of these patches compared with adjacent short, light green swards.

3.2.2 Experiment 2. Response of sheep to tall and short, dark green patches of ryegrass in a light green background sward

Experiment 3. Response of sheep to tall, light green and short, dark green patches of ryegrass in a light green background sward

3.2.2.1 Methods

In experiment 1, the input of nutrients from urination and defaecation of sheep caused the sward to grow taller in localised areas. Initially, these patches were also darker green, but as they grew older and ran out of nutrients for growth, they became a lighter shade of green. Thus, by allowing paddocks to grow for different periods after being grazed, it was possible to create either tall, light green or dark green patches. It was also possible to create short, dark green patches by fertilising the light green sward with nitrate and phosphate salts. This resulted in a rapid darkening in the shade of the grass. In experiment 2, carried out in paddock 4,

Table 3.3. Numbers of easily identifiable tall patches in paddocks and proportions of patches grazed by sheep after the termination of each experiment. The total area of tall patches was calculated by multiplying mean patch diameters by the number of tall patches and expressed as a percentage of the total paddock area (625 m^2).

Date	No. tall patches in paddock	% grazed	Diameter of tall patches (m) mean	SE	n	% paddock area occupied by tall patches
27 August 1986	31	77.4	0.8-1.0	-	2	4.0%
27 June 1987	196	71.4	0.40	0.02	10	4.0%
28 June 1987	227	71.8	0.50	0.02	10	7.3%

dark green patches were both tall and short, while in experiment 3, in paddock 1, there were tall, light green patches and short, dark green patches.

The following experiments differed from the experiment described in Chapter 2, section 2.3, in that they examined grazing behaviour over several days in response to different patch types created *in situ* rather than by transplanting turves. In addition, the physical characteristics of short swards of differing brightness were much more similar than in the section 2.3 experiment, in which the pseudostem length of transplanted short patches was exceptionally long.

Up to mid-May 1986 paddock 4 was stocked with 9-15 ewes which grazed the sward heavily. The sheep were removed and the paddock was mowed to less than 5 cm height and left ungrazed for 6.5 weeks. On 27 June 1986, eight points were selected at random in the short, light green areas of the paddock. These were clearly distinguishable from the tall, dark green patches that grew up where sheep had defaecated and urinated. These eight points were fertilised with approximately 7 g of each of ammonium nitrate (NH_4NO_3) and potassium phosphate (K_2HPO_4) salts spread over a circular area of 60 cm diameter. Similar amounts of fertiliser salts were added to these patches every 1-2 days, on three further occasions from 29 June - 2 July. In addition to the artificially fertilised patches, eight tall patches were selected at random, as were eight short, lighter green areas, 60 cm in diameter. Each patch was marked with a bamboo pole hammered into the soil and numbered. Six sward height measurements were taken in each patch on 3 July. On 4 July, vegetation in patches was sampled with a modified golf-hole corer. Live biomass was removed from the cores, and washed and dried in an oven at 80°C. Estimates of tiller density were made. Vegetation from each core taken from a tall patch was sub-divided into two samples: biomass from 0-15 cm height and the remaining biomass. Vegetation was analysed for total nitrogen, fibre and water soluble carbohydrate content (see Appendix 2.2).

Three ewes, numbers 224, 266 and 267 were placed in the paddock on 4 July 1986 and removed 13 days later on 17 July. They grazed the paddock for 10 of the 14 days. On other days they were used in experiments described in Chapter 2. Sheep 266 was observed during 15 minute observation blocks on days 1, 4, 7, 11 and 14 and her location was scored at 10 second intervals. Sward height measurements were taken in the different patches throughout the 14 day period. On 19 July, three patches of each type were selected at random and vegetation cores removed and treated as described above.

In 1987, the experiment was repeated in paddocks 1 and 4, with two different groups of sheep. Ten short, dark green patches were created in each paddock by applying fertiliser every 1-4 days from 5-14 July. Each patch received a total of four fertiliser applications. I increased the number of artificially created patches to improve the possibility of observing sheep grazing in them. The patch sites were selected at random, as were 10 tall and 10 short, unfertilised patches. At each fertilisation, all 30 patches received approximately 0.6 gallons of water each. Vegetation cores were taken from each patch on 14 July and treated as in 1986. In addition, pseudostem and lamina lengths of 10 tillers from each core were measured. Sward heights were also taken, and the fertilised patches trimmed by 2-4 cm to make their height more similar to the short, unfertilised sward. The area of the paddock occupied by the different types of patches was estimated.

On 15 July three ewes, numbers 25, 130 and 180 were placed in paddock 1 at 10:45, while the second group of ewes, numbers 88,196 and 211 were placed in paddock 4 at 12:00. Sheep were observed simultaneously for 15 minute observation blocks and their activity scored every 15 seconds.

After 3.5 hours, each patch was checked for signs of grazing. The experiments ran for six days and were terminated on 20 July. During this time further behavioural observation blocks of 15 minutes were collected, as were sward heights of different patches. Five patches were selected at random from each of the three groups in each paddock and vegetation cores were collected from each patch and analysed from 21-23 July 1987.

Procedures used in 1986 and 1987 have been summarized in Table 3.4.

3.2.2.2 Results

In paddock 1 the tall patches were light green and of similar brightness to the short background sward and in paddock 4 (1986 and 1987) they were much darker green.

The initial heights of the tall patches of ryegrass varied from 8 - 30 cm taller than the mean height of the background light green ryegrass sward (Figure 3.3). Each value represents the mean of the pooled heights taken in each marked patch. The mean heights of the short, dark green patches were 0.5 - 4 cm taller than the background sward. In all three experiments the mean heights of both patch types and the background sward declined from beginning to end, as the sward was grazed down (Figure 3.3). By the end of the 1986 experiment, the tall patches were still approximately 20 cm taller than the other two sward types, whereas in 1987 the mean heights of tall patches were only 2 - 5 cm greater than the other two sward types. After Day 2, in 1987, the mean heights of short, dark green patches were less than those of the background sward in both paddocks 1 and 4.

In all paddocks and both years, sheep grazed from all of the tall marked patches and the artificially created,

Table 3.4. Summary of pre-experiment grazing and mowing treatments and experimental designs used in July 1986 and 1987 for perennial ryegrass sward manipulation experiments.

Paddock	Period of sward regrowth prior to experiment after removal of grazing sheep	Experiment period	No. of tall marked patches	No. of short fertilised patches
<u>Experiment 2</u>				
4	19 May-4 July 1986	4 July-17 July	8	8
4	15 June-15 July 1987	15 July-20 July	10	10
<u>Experiment 3</u>				
1	13 May-15 July 1987	15 July-20 July	10	10

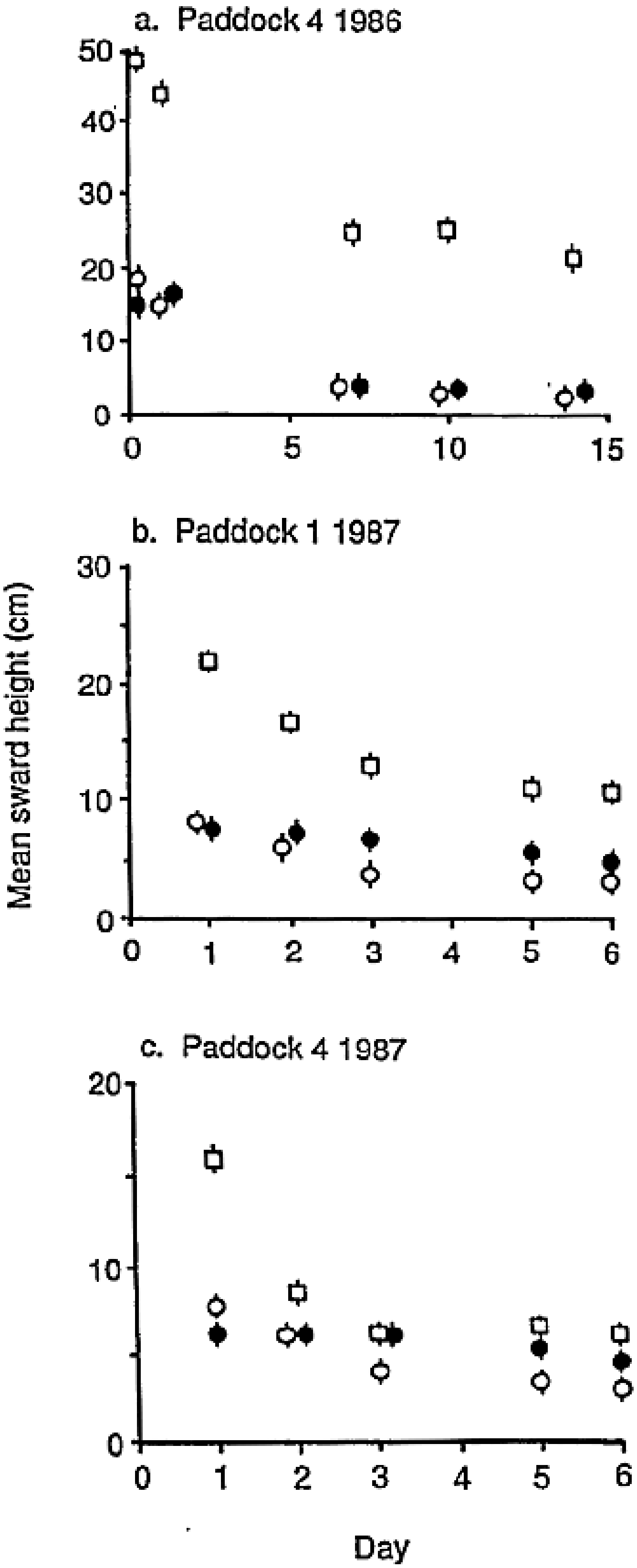

Figure 3.3. Trends in sward heights (cm) of tall dark or light green patches (□), short, dark green patches (○), and background, light green swards (●) of perennial ryegrass grazed by sheep in:.
(a) Paddock 4, 1986. (Tall patches were dark green.)
(b) Paddock 1, 1987. (Tall patches were light green.)
(c) Paddock 4, 1987. (Tall patches were dark green.)

short, dark green patches in the first two days, whereas it was 5-6 days before short, light green patches of similar size were grazed (Table 3.5). The nitrogen content of tall and short, dark green patches in paddock 4 was significantly greater than that of the short, light green background sward (Table 3.6), while in paddock 1 only the short, dark green patches had a significantly greater nitrogen content than the background sward.

The number of 10 or 15 second interval behavioural observations in which the focal sheep was grazing was calculated for each 15 minute observation period. Then, the proportion of grazing time in which a sheep fed in a particular sward type was calculated from these points. In 1986, sheep 266 was observed for a total of 234 minutes on 5 out of 14 days, while in 1987 each sheep was observed for a total of 90 - 150 minutes of grazing time, spread over six days. The proportion values from each observation period were pooled when there were no significant differences among sheep, and between experiment days 1-3 and 5-6, and mean values calculated for time spent grazing in different sward types. These mean proportions of time grazing in different sward types were compared with the proportion of total biomass made up of each sward type in different paddocks. If there was no preference for a particular sward type, then one might expect grazing time in different sward types to be proportional to biomass of each type. This is a more refined comparison than that made in experiment 1 (section 3.2.1), in which grazing time was compared with the area occupied by a tall and short sward. This did not take account of different amounts of live biomass occurring in each sward type e.g. that there may have been twice as much biomass in tall compared with short patches. Biomass of each sward type at the beginning and end of each experiment was calculated from data in Table 3.7 and counts of the number of short, dark green and tall patches.

Comparisons between mean proportions of time spent in different sward types, and their relative proportions of total biomass were made with one-sample t-tests, in which the population mean was taken as the biomass proportion of a particular sward type. Although the relative proportions of different biomass types were constantly changing, I have assumed that the ratio of proportions measured at the beginning of the experiments stayed constant from Days 1-4 (1986) and Days 1-3 (1987).

Results are summarized in Table 3.8. In paddock 1, sheep 180 was analysed separately in the tall and short, light green sward categories, since the percentage of time that she spent grazing in these sward types was significantly different from sheep 25 and 130. Sheep 25 and 130 spent significantly more time grazing in tall patches and less time in short, light green sward than expected from biomass ratios, on days 1 and 2, while all sheep spent significantly more time grazing in short, dark green patches. By days 5 and 6, the time

Table 3.5. Numbers of patches in different categories grazed as experiments progressed.

Paddock 4 1986

(n = 8 patches/category)		Number grazed			
Patch categories	Day 1		Day 3		Day 6
short/light green	0		2		8
		p = 0.013†		p = 0.004	
short/dark green	5		8		8
		p = 0.50			
tall/dark green	6		8		8

Paddock 4 1987

(n = 10 patches/category)				Number grazed				
Patch categories	Day 1		Day 2		Day 3		Day 5		Day 6
short/light green	1		3		4		9		10
		p = 0.029		p = 0.002		p = 0.005		p = 0.50	
short/dark green	6		10		10		10		10
		p = 0.50							
tall/dark green	7		10		10		10		10

Paddock 1 1987

(n = 10 patches/category)				Number grazed					
Patch categories	Day 1		Day 2		Day 3		Day 5		Day 6
short/light green	0		2		6		10		10
		p = 0.002		p = 0.003		p = 0.005			
short/dark green	10		10		10		10		10
		p = 0.105		p = 0.50					
tall/light green	7		9		10		10		10

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†All probabilities given are from Fisher's Exact Tests comparing number of patches grazed or not grazed between two different patch categories.

Table 3.6. Biochemical characteristics of perennial ryegrass in different patch types.

Paddock 4 1986	mean % Total nitrogen		mean WSC[†] (mg/g)		mean % MADF[††]	
	4 July (n = 8)	19 July (n = 3)	4 July (n = 8)	19 July (n = 3)	4 July (n = 8)	19 July (n = 3)
short/light green	0.7 (0.1)[§]	0.9 (0.1)	296* (9)	314 (9)	26.1* (0.5)	27.2 (2.2)
short/dark green	2.2* (0.2)	2.7* (0.1)	174 (20)	100* (4)	29.2 (0.6)	32.6* (1.1)
tall/dark green		0.8 (0.2)		295 (14)		29.9 (0.7)
15 cm - top of sward	1.4* (0.1)		154 (16)		28.4 (1.0)	
0 - 15 cm	0.8 (0.1)		239* (29)		29.5 (1.0)	
Paddock 4 1987	12 July (n =10)	21July (n = 5)	12 July (n =10)	21 July (n = 5)	12 July (n =10)	21 July (n = 5)
short/light green	1.2* (0.03)	1.3* (0.1)	281* (11)	297* (17)	22.3 (0.5)	28.6 (2.6)
short/dark green	3.6* (0.1)	3.9* (0.2)	96* (8)	15* (6)	23.8 (0.7)	26.8 (1.1)
tall/dark green	2.2* (0.2)	1.9* (0.1)	190* (22)	152* (27)	23.8 (0.6)	27.0 (1.2)
Paddock 1 1987	12 July (n =10)	21July (n = 5)	12 July (n =10)	21 July (n = 5)	12 July (n =10)	21 July (n = 5)
short/light green	1.0 (0.03)	1.3 (0.1)	383 (32)	175* (17)	22.7 (0.5)	24.1 (1.2)
short/dark green	3.7* (0.2)	3.8* (0.2)	111* (17)	34* (12)	23.3 (0.7)	25.1 (2.1)
tall/light green	0.9 (0.1)	1.1 (0.03)	353 (32)	257* (21)	22.5 (1.1)	26.9 (2.2)

[†] Water soluble carbohydrate (mg/g dwt of plant material).

[††] Modified acid-detergent fibre.

*Significantly different from other samples at $p < 0.05$ based on Fisher's PLSD calculations from one-way ANOVAs. Comparisons were between different patch/sward types on the same date.

[§] Figures in parentheses are standard errors of means.

Table 3.7. Physical characteristics of perennial ryegrass samples from different patch/sward types.

Paddock 4 1986	mean live biomass (g dwt m^{-2})		mean tiller density (no. tillers m^{-2} x 10^3)		mean patch diameter (m)	mean pseudostem length (cm)		mean lamina length (cm)	
	4 July (n = 8)	19 July (n = 3)	4 July (n = 3)	19 July (n = 3)					
short/light green	278 (29)†	159 (38)	11.5 (1.3)	16.7 (1.7)		-	-	-	-
short/dark green	292 (41)	165 (13)	12.0 (1.9)	20.8* (1.9)	c 0.60	-	-	-	-
tall/dark green	981* (100)	764*(100)	8.5 (0.9)	12.9 (0.6)	c 0.60	-	-	-	-
Paddock 4 1987	12 July (n =10)	21 July (n = 5)	12 July (n =10)	21 July (n = 5)	12 July (n =10)	12 July (n = 60)	21 July (n = 30)	12 July (n = 60)	21 July (n = 30)
short/light green	101* (4)	75 (6)	10.0 (0.8)	10.1* (0.9)	-	1.1 (0.1)	0.8* (0.1)	4.7 (0.2)	4.3* (0.2)
short/dark green	154* (8)	87 (9)	13.3 (1.1)	15.8* (1.2)	0.54 (0.03)	1.5 (0.1)	1.9 (0.1)	5.4 (0.2)	2.5* (0.2)
tall/dark green	357* (28)	185* (24)	20.8* (2.0)	21.8* (2.1)	0.58 (0.02)	2.7* (0.2)	2.3 (0.2)	9.0* (0.5)	3.5* (0.2)
Paddock 1 1987	12 July (n =10)	21 July (n = 5)	12 July (n =10)	21 July (n = 5)	12 July (n =10)	12 July (n = 60)	21 July (n = 30)	12 July (n = 60)	21 July (n = 30)
short/light green	172 (17)	113 (14)	10.5 (1.2)	12.0 (1.0)	-	1.5 (0.1)	0.9* (0.1)	5.8 (0.2)	4.3 (0.3)
short/dark green	211 (48)	93 (10)	11.4 (1.2)	15.4 (1.9)	0.62 (0.01)	1.9 (0.1)	1.9 (0.1)	6.8 (0.3)	2.4* (0.2)
tall/light green	550* (50)	196* (18)	14.8* (1.0)	14.2 (2.0)	0.59 (0.02)	3.9* (0.3)	2.1 (0.2)	13.6* (0.5)	5.0 (0.4)

*Significantly different from all other groups sampled on the same date at $p < 0.05$ based on Fisher's PLSD calculations from one-way ANOVAs.

†Figures in parentheses are standard errors of means.

Table 3.8. Comparison of observed proportions of time spent grazing by sheep in different sward types with expected values based on biomass ratios of those sward types.

	Patch/sward type	Sheep	Observed % grazing time mean	S.E.	n†	Expected % grazing time	t-value
Paddock 4, 1986							
Day 1	Tall/dark green	266	74.8	6.2	5	57.0	2.87*
	Short/dark green	"	1.1	1.1	5	0.3	0.72 n.s.
	Short/light green	"	23.8	5.4	5	42.7	3.56*
Day 4	Tall/dark green	266	20.3	6.8	3	57.0	5.36*
	Short/dark green	"	7.2	1.6	3	0.3	4.18*
	Short/light green	"	71.7	5.4	3	43.0	5.34*
Days 5-14	Tall/dark green	266	21.9	4.2	9	66.0	8.36***
	Short/dark green	"	0.4	0.3	9	0.2	0.64 n.s.
	Short/light green	"	77.8	4.2	9	33.8	10.56***
Paddock 4, 1987							
Days 1-3	Tall/dark green	all	58.6	9.7	7	23.1	3.67*
	Short/dark green	"	11.1	1.8	7	0.5	5.95**
	Short/light green	"	30.3	8.0	7	76.4	5.80**
Days 5-6	Tall/dark green	all	14.2	2.9	13	17.4	1.09 n.s.
	Short/dark green	"	9.2	2.6	13	0.4	3.39**
	Short/light green	"	76.6	2.8	13	82.2	1.98 n.s.
Paddock 1, 1987							
Days 1-3	Tall/light green	25,130	71.0	6.6	8	45.5	3.84**
	Short/dark green	"	14.0	4.7	8	0.4	2.86*
	Short/light green	"	14.0	4.2	8	54.2	9.34***
Days 1-3	Tall/light green	180	19.9	9.0	3	45.5	2.85 n.s.
	Short/dark green	"	36.9	7.2	3	0.4	5.03*
	Short/light green	"	43.0	3.0	3	54.4	3.89 n.s.
Days 5-6	Tall/light green	all	29.7	9.6	13	31.2	0.17 n.s.
	Short/dark green	"	5.4	2.5	13	0.4	1.96 n.s.
	Short/light green	"	64.9	9.0	13	68.4	0.38 n.s.

†Each sample measurement represents 1 x 15 minute observation period.

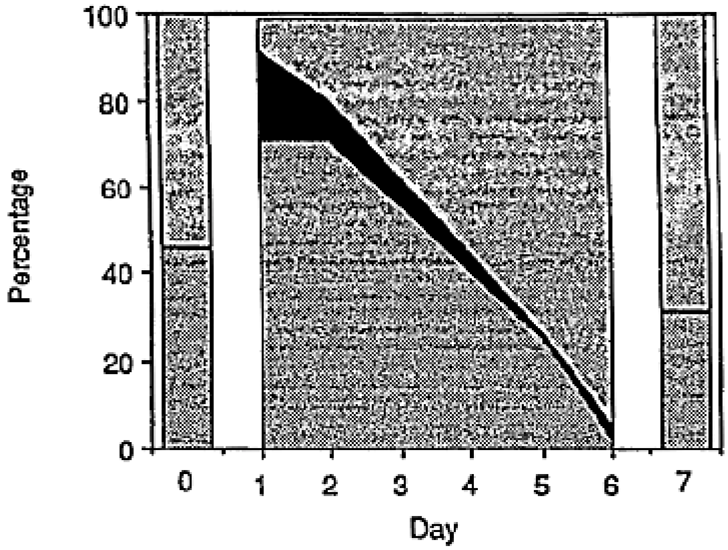
spent grazing in different sward types was not significantly different from expected values based on biomass ratios.

Similar results were obtained from paddock 4 in 1987, in that all sheep initially preferred to graze in tall and short, dark green patches, and avoid light green background sward. On days 5 and 6 however, the trend had switched, in that time spent in tall and short, light green sward was not significantly different from biomass ratios, while sheep still preferred short, dark green patches. In 1986, sheep 266 preferred tall patches on day 1, but had switched her preference to short patches by day 4. This continued for the remainder of the experiment. It was only on day 4 that a preference for short, dark green patches was detected, but it seems likely that if behavioural observations had been collected on days 2 and 3, then further indications of this preference would have been detected.

Data for two individual sheep are presented in Figure 3.4, illustrating the trends in switching preferences for different sward types. The relative preference of sheep for tall versus short, dark green patches between days 1 to 3 was assessed. The ratio of the observed percentage of grazing time to the expected percentage of grazing time was calculated for each 15 minute observation period sample (Tables 3.8 and 3.9). The expected value was based on either the proportion of total biomass or the paddock area occupied by the different types of patch. Means of these ratios were compared between patch types and with an expected ratio of 1 which was taken as sheep expressing no preference (Table 3.9). In Paddock 4, data were pooled among sheep, as the number of 15 minute observation periods collected for each sheep was not sufficient for individual comparisons to be made. In Paddock 1, sheep 180 was excluded from the analysis, since she only had a significant preference for short, dark green patches (Table 3.8). In 3 out of 4 paired t-test comparisons, sheep had a significantly greater preference for short, dark green patches compared with tall patches (Table 3.9). However, in Paddock 1, when expected values were based on area proportions, patch preferences were not significantly different, because in some observation periods, the sheep did not graze at all in short, dark green patches and always grazed for some time in tall patches. All of the mean ratios given in Table 3.9 were significantly greater than 1 when compared in one sample t-tests, at $p < 0.05$ to $p < 0.001$ depending upon the comparison.

In Paddock 4 in 1986 and 1987 the tall patches were higher in nitrogen and lower in water soluble carbohydrate content than the lighter green background sward and the initial preference of sheep for tall patches may have been related to this (Table 3.6). However, in Paddock 1 in 1987, the tall patches were similar to

a. Sheep 130 Paddock 1 1987



b. Sheep 196 Paddock 4 1987

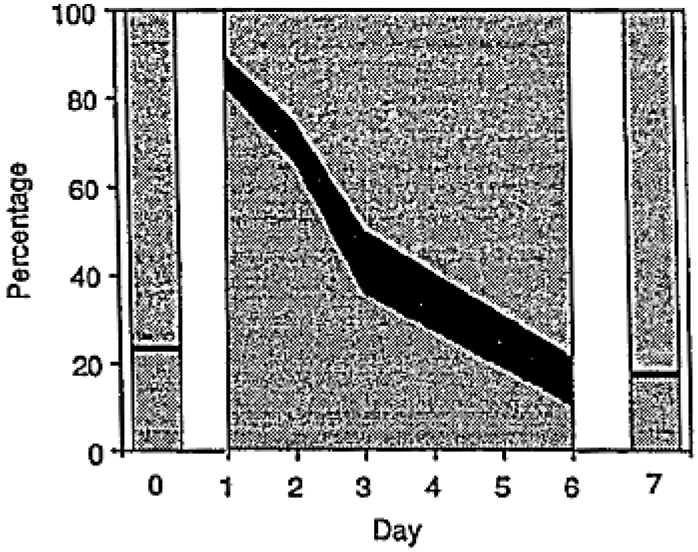


Figure 3.4. Proportions of different types of perennial ryegrass swards contributing to total live above-ground biomass (g dry weight) in:
(a) Paddock 1 (Tall patches were light green.), (b) Paddock 4 (Tall patches were dark green.) at the beginning (Day 0) and end (Day 7) of experiments carried out in July 1987.
From Day 1 - Day 6, the percentages of grazing time spent in different sward types are given for (a) sheep 130, (b) sheep 196.
(Percentages of ryegrass biomass were based on biomass determinations (g dwt m^{-2}) of different sward types and estimates of areas occupied by those sward types. ▨ – tall patches; ■ –short, dark green patches; ⊡ –short, light green background sward. See text for details of methods used to assess grazing times.)

Table 3.9. The relative preference of sheep for short, dark green patches and tall patches.

	Ratio of observed proportion of grazing time: expected proportion of grazing time					
	Expected value based on biomass proportions of patch types			Expected value based on proportion of total paddock area comprised of patches		
	Mean of ratios	S.E.	n	Mean of ratios	S.E.	n
Experiment 2, Paddock 4						
Patch type						
Tall dark green	2.5	0.4	7	7.7	1.2	7
Short dark green	27.9	4.5	7	27.9	4.5	7
		t = 6.97***†			t = 3.87**	
Experiment 3, Paddock 1††						
Patch type						
Tall light green	1.6	0.2	8	3.4	0.3	8
Short dark green	34.5	11.7	8	27.6	9.4	8
		t = 2.51*			t = 1.55 n.s.	

†Paired t-tests were performed on log-transformed data.

††Sheep 180 was excluded from the analysis because her behaviour differed significantly from other sheep.

the short, light green sward in nitrogen and water soluble carbohydrate content. In both years ryegrass in artificially created short, dark green patches had a much higher nitrogen content than both other types of sward. Initial preference of sheep for these patches was reflected in their being grazed at the same rate as the marked tall patches (Table 3.5) and their mean height declining below that of short, light green sward two days after the experiment began (Figure 3.3).

Reasons for switching from tall to short light green sward in the case of Paddock 4 (1986) may have been related to the low nitrogen content of the bottom half of the vegetation, but this could not have been the case in Paddock 1. In this paddock, the increased likelihood of biting into tough pseudostem may have been a factor in causing the sheep to switch. The effect of pseudostem length on intake was shown in the experiment in section 2.3. The final lamina lengths in tall patches (21 July 1987) were similar to or less than those in short, light green swards in Paddocks 1 and 4 respectively (Table 3.7) while pseudostem lengths were significantly greater in tall patches compared with short swards. In Paddock 4 (1987), in which grazing time in tall and short, light green sward was proportional to biomass ratios (Table 3.8), the nitrogen content of ryegrass in tall patches was still significantly greater at the end of the experiment (Table 3.6).

Additional reasons for switching may have been related to changes in the relative biomass of different patch types during the experiments. Greenwood & Elton (1979) reviewed some of the studies in which prey selection was shown to depend on the relative frequency of availability of different prey types. It would be of interest to extend their model to a herbivory situation, analysing whether there are changing preferences for tall patches and short, dark green patches in relation to the relative abundance of each sward type. However, this type of analysis was not appropriate for the present experiments, because there were changes in the nature of the "prey" (sward types) in addition to changes in their relative abundance. Even so, it appeared that the sheep's preference for short, dark green patches could not have been caused by their abundance as has been observed in some foraging situations (Greenwood & Elton 1979); this patch type was not very abundant.

In summary, sheep initially preferentially grazed from tall patches of ryegrass regardless of their nutritional value and brightness i.e. dark green or light green. They also grazed preferentially from short, dark green patches of ryegrass that were nutritionally better than the light green background sward. However, preferences changed by days 5 and 6 in all experiments and sward types were either grazed in proportion to their biomass, or sheep switched their preference to short, light green background swards. The latter result was probably caused by sheep avoiding tough pseudostem. Results from these and other experiments in

Table 3.10. Summary of experimental results from Section 3.2.

Experiment number	Experiment tested behavioural response of sheep to:	Observed preference
1	Tall, dark green patches and short, light green background sward.	Tall, dark green patches.
2	Tall, dark green patches and short, dark green patches versus short, light green background sward.	Tall and short, dark green patches.
3	Tall, light green patches and short, dark green patches versus short, light green background sward.	Tall, light green and short, dark green patches.

section 3.2 are summarized in Table 3.10.

3.3 The relationship between brightness of perennial ryegrass and its biochemical characteristics

3.3.1 Methods

The enormous variation in brightness (dark green/light green) of perennial ryegrass within paddocks was created by nutrient inputs either from sheep or fertiliser salts, to paddocks which had otherwise received no artificial fertiliser. A possible basis of the consistent preference of sheep for darker green areas of ryegrass was investigated in the experiment described below, which aimed at determining whether there was a relationship between brightness and nutritional quality of ryegrass. A range of brightnesses in ryegrass was created by differential fertiliser applications. The levels of brightness were quantified and related to biochemical analyses of the vegetation.

On 9 June 1987, 35 trays of perennial ryegrass (var. Parcour) were sown at 2 g seed per tray. Seven trays were assigned to one of five fertiliser treatment levels:

(1) Control - received no fertiliser

(2) Low treatment - 0.5 g ammonium nitrate (NH_4NO_3) salts, 0.5 g potassium phosphate (K_2HPO_4) salts

(3) Medium 1 treatment - 1 g of each of NH_4NO_3 and K_2HPO_4 salts

(4) Medium 2 treatment - 2 g of each of NH_4NO_3 and K_2HPO_4 salts

(5) High treatment - 5 g of each of NH_4NO_3 and K_2HPO_4 salts.

From 9 June to 15 July, groups of trays received the above amounts of fertilising salts on 4-5 occasions, every 4-12 days. All trays were trimmed to 5 cm height on 9 and 15 July 1987.

Brightness, or the total amount of light reflected from trays of ryegrass receiving different amounts of fertiliser, was characterized by two methods:

(1) Analysing photographic transparencies of ryegrass with a Macbeth TD 504 Densitometer.

(2) Measuring the reflectance spectra of ryegrass using an ISCO model SR Spectroradiometer.

The densitometry method was more versatile, since either colour slides or black and white negatives of ryegrass trays could be taken and analysed later. Use of spectroradiometry was more limited since readings had to be taken on live biomass. However, spectroradiometry allowed characterization of colour as well as brightness. The spectroradiometer was available only in September 1987.

The densitometer measured the brightness (amount of light reflected) from different trays of ryegrass. A transmission densitometer passes a beam of light through the transparency and characterizes the "blackness" of images with a density reading (Wakefield 1971).

$$\text{Density} = \log_{10} (\text{Opacity})$$

$$\text{Opacity} = \text{inverse of transparency}$$

$$= \frac{L_i \text{ (incident light)}}{L_t \text{ (transmitted light)}}$$

The higher the density, the darker or more opaque the image on the transparency and the lower the total amount of light reflected from that image.

On 17 July, photographs were taken of trays from different treatment groups in the greenhouses at Wytham Field Station under natural lighting conditions. A Hasselblad twin lens reflex camera was used with colour slide film and black and white print film. Relative differences between the brightness of grass trays picked out by the densitometer were expected to vary according to the sensitivity of different film emulsions. By using two types of film it was possible to compare tray to tray variation in brightness between films having different sensitivity to brightness.

In order to extend the range of hues and brightnesses of ryegrass, cores were taken from "natural" dark green ryegrass patches in paddock 4 and also photographed in the geenhouse. Trays of ryegrass from different fertiliser treatments were included in the same photographic frame in order to control for varying light conditions between frames. In addition, a Kodak grey card of known reflectance (18%) was photographed in each frame to allow between-frame calibration and comparison if desired.

The live biomass from three replicate trays in each treatment group was harvested, washed and dried at 80°C in a drying oven before being analysed for total nitrogen, fibre and water soluble carbohydrate content (see Appendix 2.2 for procedures used). In addition, fresh weights of sub-samples of biomass were taken on a Sartorius analytic balance. The dry weights of these samples were taken later and water content was calculated.

From 11-14 September and on 23 September, the reflectance spectra of the ryegrass from remaining trays in each group was characterized using the spectroradiometer equipped with a 3 foot long fibre optics extension probe. Spectral intensity readings ($\mu W\ cm^{-2}\ nm^{-1}$) of the amount of light relected in 12.5 nm wavelength bands from 400 - 750 nm were collected from ryegrass samples. Correction factors used were calculated by

ISCO, Nebraska, U.S.A. in June 1986. Measurements were made in growth room B in Wytham Field Station because of its constant light conditions.

Ryegrass leaves measured were cut from a replicate tray to 3 cm above soil level. Depending upon fertiliser treatments, leaves were 8 - 15 cm long. Dead leaves were removed and the remaining bunch of leaves was arranged on a stiff piece of white card approximately 15 cm x 15 cm and stuck down at each end with sticky tape. No white card was visible through the leaves which covered an area of 8-15 cm x 6 cm. The card was then positioned under the fibre optic probe attached to the spectroradiometer. The height of the probe above the card was held constant by permanently clamping the probe in position. The probe was surrounded by a 2 cm long cardboard tube painted matt black on its interior surface. Thus, when positioned above the sample, the only rays of light reaching the probe head were those which travelled parallel to the walls of the tube after being reflected directly upwards from the ryegrass beneath the probe (Figure 3.5). These arrangements ensured that the light absorbed by the probe could be compared between samples.

In addition to characterizing spectra of ryegrass from treatment groups, ryegrass cores were sampled from dark green and light green areas of paddock 4 and from a tray used in experiments described in Chapter 4. After each ryegrass sample was measured with the spectroradiometer, it was washed, dried and chemically analysed.

3.3.2 Results

The relationships between fertiliser treatment and chemical characteristics of ryegrass are shown in Table 3.11. The trays receiving least amounts of fertiliser had the lowest nitrogen content and the highest water soluble carbohydrate contents. Interestingly, water content of ryegrass from trays measured in July 1987, and subjected to similar growth conditions, also varied according to fertiliser treatment.

Densitometer readings were taken from film positives and negatives of groups of ryegrass trays from all treatments except for the Medium 2 group which was not photographed. These trays appeared to be of similar brightness to the High treatment group trays, and were excluded on these grounds, which was unfortunate, since brightness data were lost for no particularly good reason. Readings varied significantly among trays ' from different fertiliser treatment groups and ryegrass cores from the paddocks (Agfachrome colour slide film: $F_{4,22} = 31.1^{***}$). The darkest green trays were from the high level fertiliser group and had the highest density readings (Table 3.11a). Regressions of densitometer readings on total nitrogen and water soluble

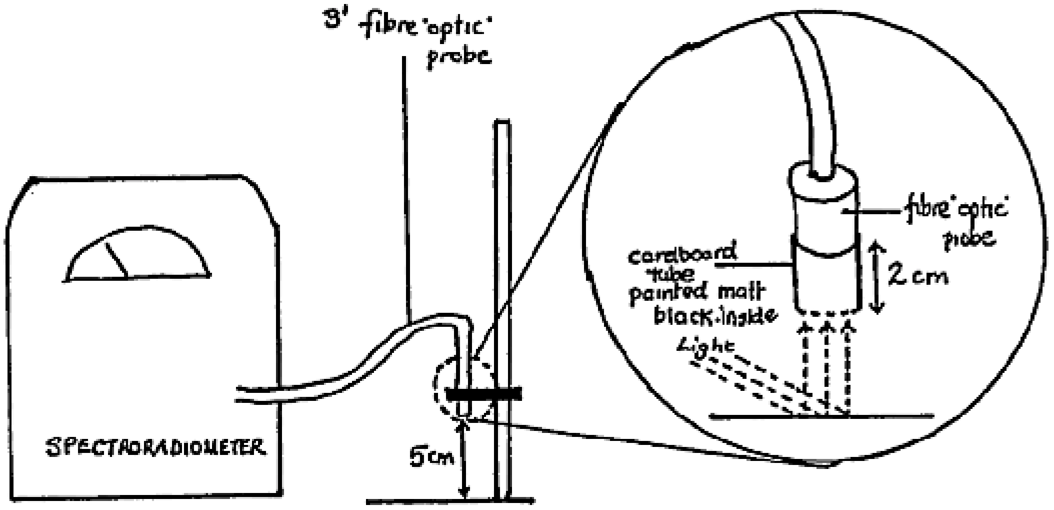


Figure 3.5. Design of equipment set-up for the determination of the reflectance of incoming radiation from samples of perennial ryegrass taken from different fertiliser treatment groups.

Table 3.11 a. Brightness and chemical characteristics of perennial ryegrass grown under different fertiliser treatment regimes, measured in July 1987. (chemical analyses: n = 3 for fertiliser treatments and n = 5 for ryegrass samples from paddocks; densitometer readings: n = 3 - 6 depending upon size of grass tray in slide).

Fertiliser treatment/ sample source	Densitometer reading: colour slide film		Water content (% fresh wt)		Total nitrogen (% dry wt)		WSC† (mg/g dry wt)		% MADF††	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
No fertiliser	2.06	0.02	85.7	0.2	1.7	0.1	229.4	6.2	20.6	0.8
Low level	2.37	0.05	89.6	0.3	2.5	0.1	73.0	19.5	25.3	2.2
Medium 1 level	2.56	0.05	89.2	0.7	3.0	0.3	48.3	15.3	23.9	0.7
Medium 2 level	-	-	90.7	0.4	4.4	0.2	32.9	12.5	23.1	0.9
High level	2.66	0.04	90.9	0.9	5.1	0.1	15.1	2.6	21.9	0.3
		$F_{4,10}$:	13.8***		71.8***		45.9***		2.4 n.s.	
		Fisher's PLSD:	1.8		0.52		40.3		3.7	
Paddock 4 ryegrass										
Dark green core	2.70	0.11	83.6	0.7	3.9	0.2	15.0	6.0	26.8	1.1

† Water Soluble Carbohydrate content

†† Modified acid-detergent fibre

Table 3.11 b. Brightness and chemical characteristics of perennial ryegrass grown under different fertiliser treatment regimes, measured in September 1987 (n = 1 for each chemical analysis and n = 3 or 1 for peak reflectance values).

Fertiliser treatment/ sample source	Reflectance at 575 nm ($\mu W\ cm^{-2}\ nm^{-1}$)		Total nitrogen (% dry wt)	WSC[†] (mg/g dry wt)	% MADF[††]
	mean	SE			
No fertiliser	.248	.000	1.58	152.0	25.7
No fertiliser	.202	.011	1.50	210.4	22.9
Low	.228	.020	2.02	160.2	22.2
Medium 1	.155	.007	2.20	165.8	23.9
Medium 2	.157	.005	3.50	21.2	23.9
High	.161	.006	4.21	55.1	22.5
Paddock 4 ryegrass					
Light green	.177	-	1.90	201.6	19.9
Dark green	.106	-	5.61	39.2	17.2
Dark green	.101	.003	5.28	46.6	17.0
Ryegrass turf used in Chapter 4 exp'ts	.132	.006	3.77	5.9	27.8

[†] Water Soluble Carbohydrate content

[††] Modified acid-detergent fibre

carbohydrate content of ryegrass were highly significant (nitrogen: regression $F_{1,11} = 29.7^{***}$, $r = 0.85^{**}$ df = 11; water soluble carbohydrate: regression $F_{1,11} = 100.4^{***}$, $r = 0.95^{**}$ df = 11) (Figure 3.6). Regressions of density on water content and modified acid-detergent fibre (MADF) were not significant (water content: regression $F_{1,11} = 3.1$ n.s., $r = 0.47$ n.s. df = 11; MADF: regression $F_{1,11} = 1.7$ n.s., $r = 0.37$ n.s. df = 11).

Results from black and white negatives were similar. However, because negatives were measured rather than positives, trays from the high fertiliser treatments were the lightest shade of grey and had the lowest readings (mean density = 0.22, n = 3), while those from the control group receiving no fertiliser were the darkest and had the highest densitometer readings (mean density = 0.39, n = 6). There was significant variation in density among different fertiliser treatment group ($F_{4,16} = 62.1^{***}$), and regressions of density readings on chemical characteristics were similar to those for colour slide readings (nitrogen: regression $F_{1,11} = 19.9^{***}$, $r = 0.80^{**}$; water soluble carbohydrate: regression $F_{1,11} = 72.9^{***}$, $r = 0.93^{**}$; water content: $F_{1,11} = 1.4$ n.s., $r = 0.33$ n.s.; MADF: $F_{1,11} = 3.2$ n.s., $r = 0.48$ n.s., df = 11 in all cases).

Reflectance spectra of ryegrass from two different fertiliser treatments and dark green patches in paddock 4 are shown in Figure 3.7. They were determined with the spectroradiometer. The shape of the curve was very similar for all ryegrass samples measured and the peak value of spectral intensity ($\mu W\ cm^{-2}\ nm^{-1}$) occurred at 575 nm in all cases. Thus, the curve for each sample measured has been characterized in Table 3.11b by its peak reflectance value at 575 nm. The main visual difference among samples was not in the hue or colour, but brightness. Samples from trays receiving no fertiliser and from light green areas of the paddock were the brightest, in that they reflected most incoming radiation from the lights in the growth room and their peak reflectance values were the highest. Ryegrass from trays receiving high amounts of fertiliser salts and from dark green areas of the paddock, which had been urinated upon by sheep, reflected the least amount of incoming radiation. The relationship between the peak reflectance value and chemical composition of ryegrass is shown in Figure 3.8. The regressions of peak reflectance on nitrogen content and water soluble carbohydrate content were significant (nitrogen: regression $F_{1,8} = 23.2^{**}$ $r = 0.86^{**}$ df = 8; water soluble carbohydrate: regression $F_{1,8} = 6.9^{*}$ $r = 0.68^{*}$ df = 8), while that on fibre (MADF) was not ($F_{1,8} = 2.1$ n.s. $r = 0.46$ n.s. df = 8).

Although there was no significant relationship between brightness of ryegrass and water content, there was some suggestion that within groups of ryegrass receiving similar inputs of water, increased brightness

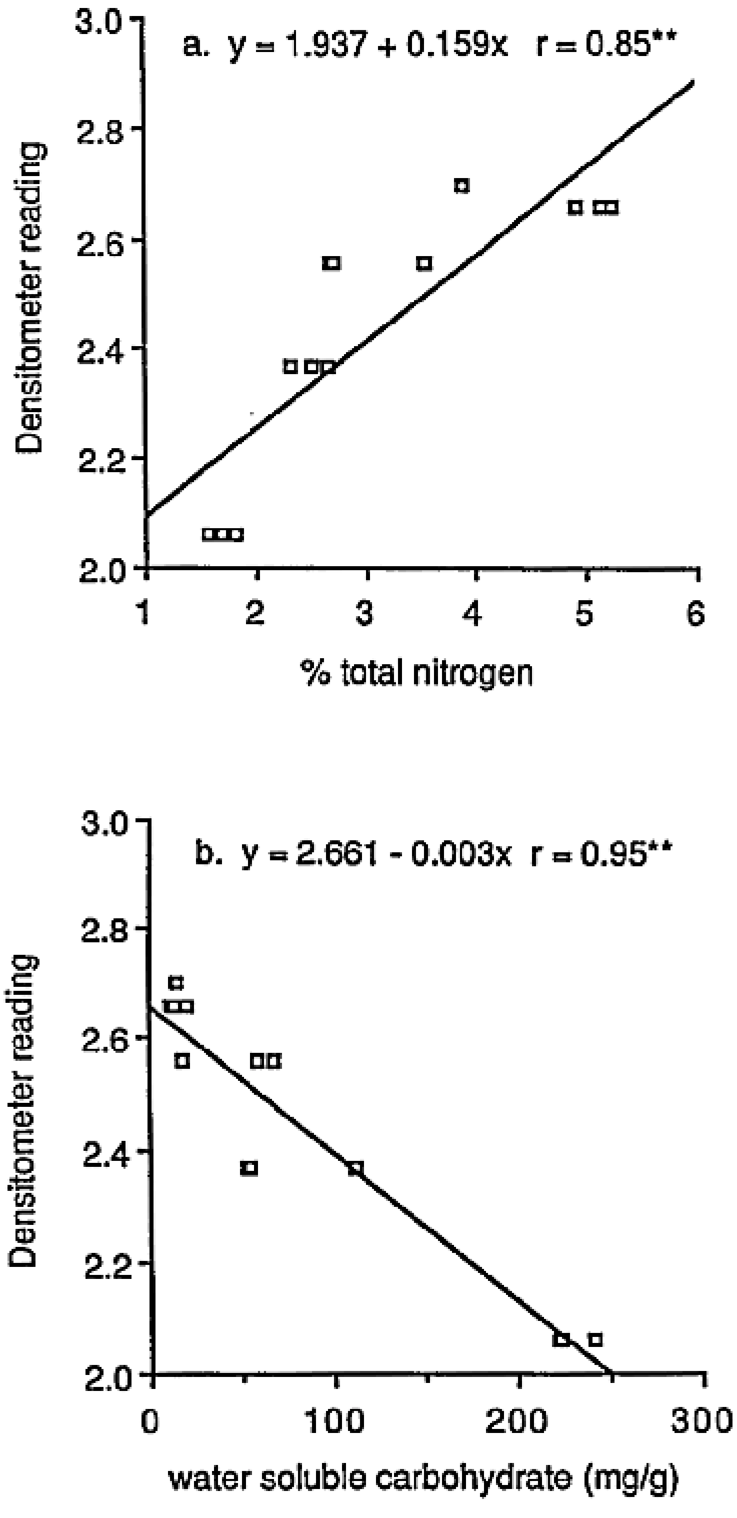


Figure 3.6. Relationships between densitometer readings and
(a) total nitrogen content (% dry weight),
(b) water soluble carbohydrate content (mg/g dry weight)
of perennial ryegrass. (Lines are simple regressions.)

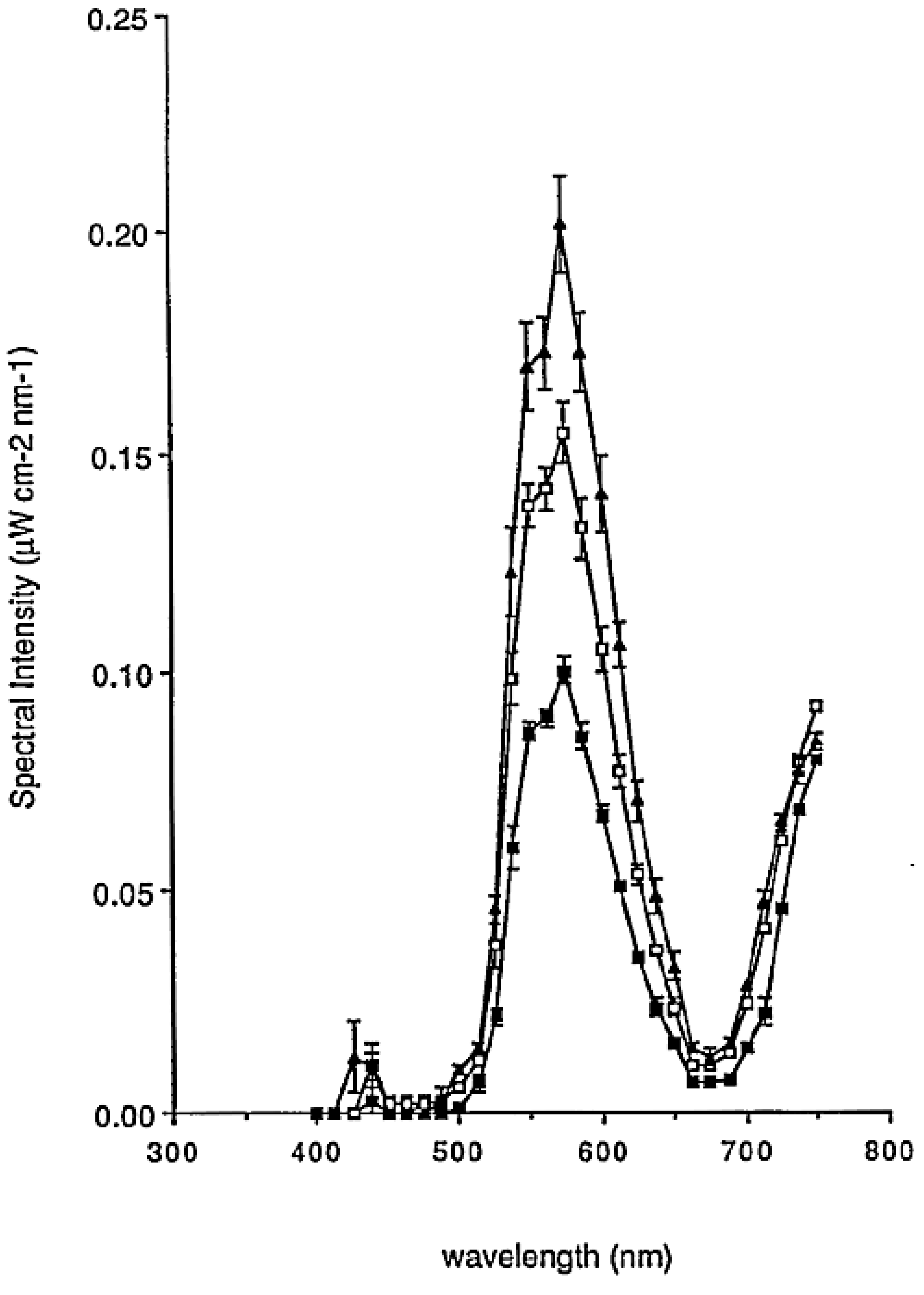


Figure 3.7. Spectral intensity (µW cm^{-2} nm^{-1}) showing amount of incoming radiation reflected from dark green ryegrass from paddock 4 (■), ryegrass in the medium 1 fertiliser group (□), and ryegrass in the control group receiving no fertiliser (▲). (mean ± SE, n = 3).

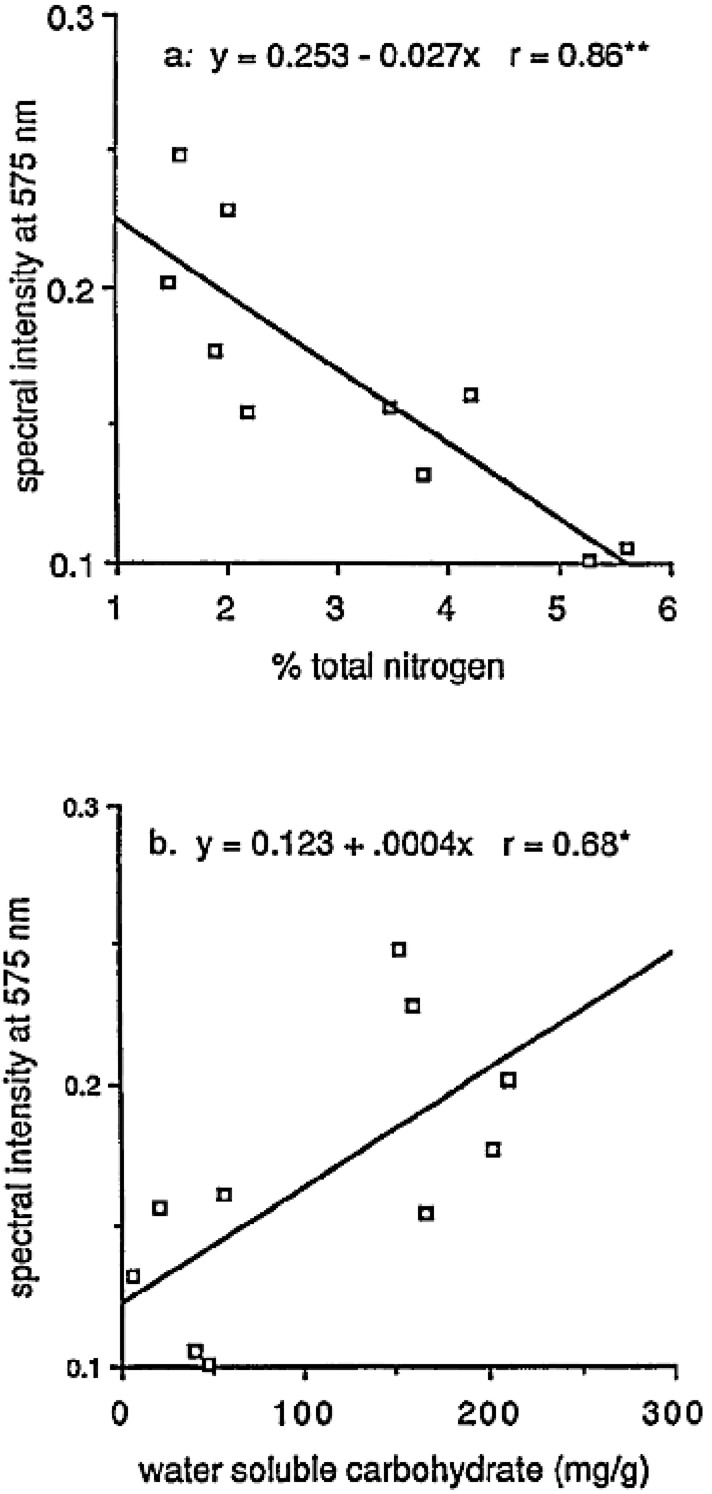


Figure 3.8. Relationship betwen spectral intensity (amount of light reflected - µW cm^{-2} nm^{-1}) and
(a) total nitrogen content (% dry weight),
(b) water soluble carbohydrate content (mg/g dry weight)
of perennial ryegrass. (Lines are simple regressions.)

may have been negatively correlated with water content. In Table 3.11a the darkest trays, receiving the greatest amounts of fertiliser, had the highest water content. When the water content of the dark green core removed from the paddock was excluded from a regression of densitometer reading on water content, a significant result was obtained ($F_{1,10} = 40.5^{***}$, $r = 0.90^{**}$ df = 10).

In summary, the brightness of ryegrass measured with either a transmission densitometer or spectroradiometer varied significantly in response to different levels of fertilisation. There was a strong relationship between brightness and total nitrogen and water soluble carbohydrate content of biomass: darker ryegrass had a higher nitrogen content and lower water soluble carbohydrate content than lighter green (brighter) ryegrass. There was no significant relationship between brightness and fibre content of ryegrass, or between "hue" (colour or shade) of green and nutritional content of ryegrass.

3.4 Responses of sheep in indoor choice trials between dark green and light green trays of ryegrass

3.4.1 Methods

The results of section 3.3 showed a strong relationship between the brightness of ryegrass and its nitrogen and water soluble carbohydrate content. Thus, it was possible that in the field experiments described in section 3.2, sheep were responding to variations in brightness of ryegrass because brightness was a cue to nutritional quality. Therefore, it was of interest to determine how fixed their preference for dark green ryegrass was. In the experiment described in this section the aim was to determine what decision a sheep would make when given a straight choice between two ryegrass trays of different brightness. I predicted that they would prefer darker green trays, since this would reflect field observations.

In January 1986, a pen was set up in the sheep shed at Wytham Field Station in which sheep were allowed access to an inner pen from an outer holding pen when a gate was raised (Figure 3.9). Two trays of perennial ryegrass which differed in brightness were placed at the far end of the inner pen. When the gate was raised, the sheep entered the pen and was allowed 30 seconds to graze from either or both trays. The amount of time spent grazing in different trays was noted as was the number of times that the sheep switched back and forth. At the end of the 30 second period, the sheep was removed from the paddock. The two trays were then removed from the inner pen and replaced with two more trays. After a three minute interval, the sheep was again allowed to feed from the trays for 30 seconds. Two further trials of 30 seconds at three minute intervals were carried out. Fifteen sheep were tested in this way. The sheep were deprived of food for 3-5 hours prior

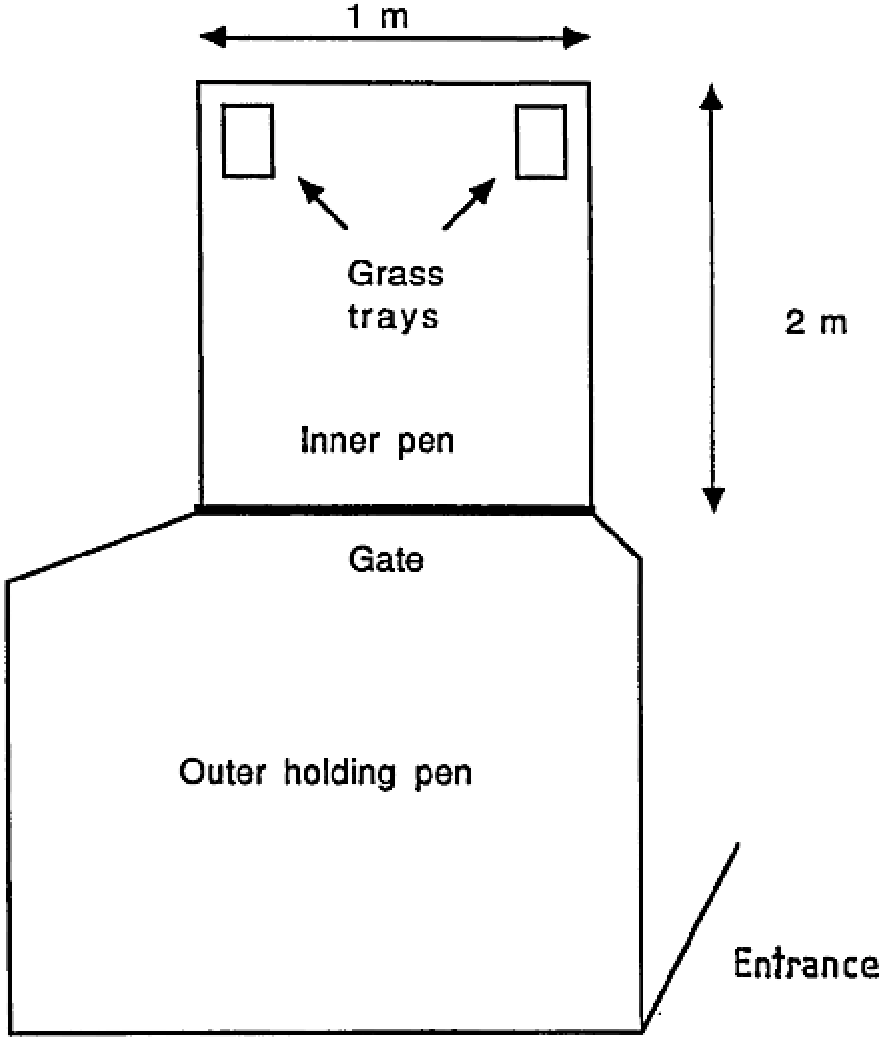


Figure 3.9. Pen set-up for test of preferences for trays of perennial ryegrass varying in brightness.

to testing. Trials were run from 28 January - 17 February 1986.

Trays of ryegrass used were planted from 11-19 September 1985, at 0.8g seed (var. Parcour) per tray, and were 20 cm x 35 cm in size. Light green trays of ryegrass were not fertilised and were covered with black polythene sheeting three to four days prior to the choice trials. This resulted in etiolation and lightening of leaf colour. Dark green trays were fertilised with either Maxicrop liquid fertiliser on 23 and 27 January 1986 or with 2 g of each of NH_4NO_3 and KH_2PO_4 salts on 21 January 1986. Before being fed to sheep, all trays were trimmed to 10 cm height.

The relative brightness of the grass trays was assessed using a densitometer to read values from slides of trays. Replicate trays were harvested and analysed for water, nitrogen and fibre content, as well as strength of leaves, characterized as the amount of force in grammes needed to break a leaf that registered on a pesola scale. This additional parameter was measured because the apparatus was available at the time of this experiment.

3.4.2 Results

During the first trial significantly more sheep selected the dark green ryegrass tray to graze from first (sign test: $p = 0.018$, $n = 15$) (Figure 3.10). However, in further trials, there was no significant difference between the number of sheep selecting a light green or dark green tray to graze from first (trial 2: $p = 0.85$; trials 3 & 4: $p = 0.50$) (Figure 3.10). The decrease over the four trials in the number of sheep feeding from dark green trays first was significant. This decrease was tested by regressing choice (1 = dark green, 0 = light green) on trial number for each sheep. The mean of the 15 regression slopes was calculated, compared with a population mean of zero and found to be significantly different ($t = 2.38^*$ $df = 14$), indicating that the first choice of tray was not constant over the trials.

The amount of time spent grazing in dark green trays in each 30 second period was compared with an expected allocation of 50% of time feeding in each tray if the sheep had no preference. Time spent grazing in light green trays was subtracted from time in dark green trays for each sheep. The mean difference for each trial was compared with a population mean of zero in a one-sample t-test. In trials 1 and 4 the difference was significantly greater than zero ($t_{trial\ 1} = 5.2^{***}$ $df = 14$; $t_{trial\ 4} = 2.96^*$ $df = 14$), indicating that sheep spent more time feeding from dark green trays. In trials 2 and 3, the differences were not significantly greater than zero ($t_{trial\ 2} = 1.33$ n.s. $df = 14$; $t_{trial 3} = 1.79$ $df = 14$), and sheep did not spend more time than expected feeding in either dark or light green trays. When individual sheep were compared across trials, only 4 out of

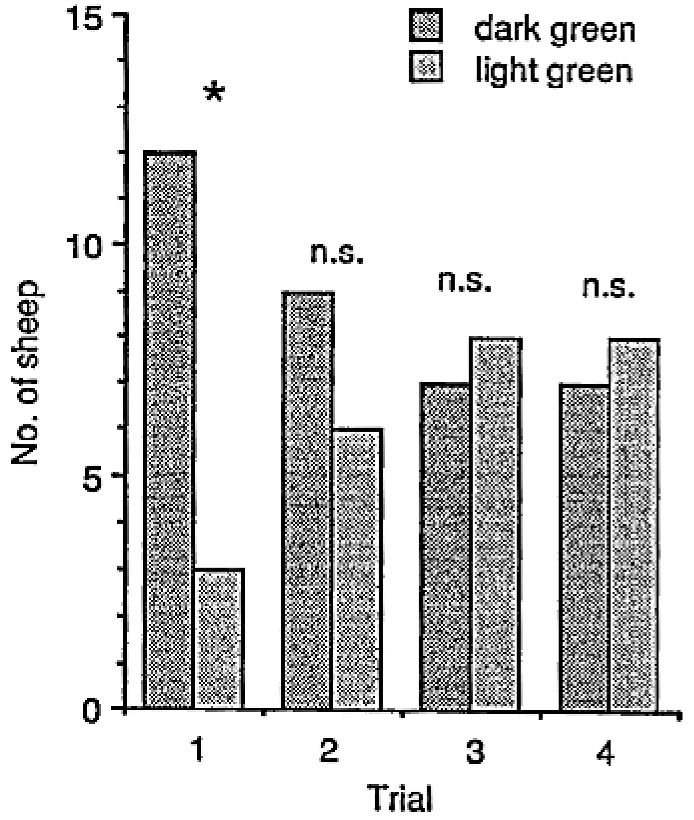


Figure 3.10. Number of sheep choosing to graze first from dark green (▩) or light green (▨) trays of perennial ryegrass. Each sheep was tested over 4 consecutive trials. (n = 15 sheep tested.)

15 spent significantly more time feeding from dark green trays, while the others showed no consistent preferences. Mean values of time spent grazing in trays of different brightness are shown in Figure 3.11.

Densitometer readings for trays were obtained from slides (Table 3.12), and as expected, densities were highest for dark green trays. The chemical content of dark green and light green trays varied enormously (Table 3.12). There were in effect two categories of "dark" green trays on offer to sheep with widely different nitrogen contents. These categories were related to whether trays received liquid fertiliser and were kept outside the greenhouse until January 1986, in which case they had a lower nitrogen content than those trays brought into the greenhouse and fertilised with nitrogen salts. While the fibre content of the light green grass was significantly higher than that of the two groups of dark green grass, the nitrogen content was in-between. Also, the breaking strength or "toughness" of dark green grass was greater. The correlation between brightness (densitometer reading) of ryegrass and its nitrogen and water content did not hold in these trials. No record was kept of which dark green trays were offered to which sheep. Thus, it was not possible to relate switches in preferences for dark and light green trays to the sheep feeding from the different groups of dark green trays.

In summary, although significantly more sheep initially grazed from darker green trays of ryegrass, this preference decreased over the following three trials. Sheep grazed from both dark and light green trays when given the opportunity to do so in a 30 second grazing trial. The relationship between brightness and nitrogen content was not consistent. In addition, the dark green grass trays which had the lower fibre content (most digestible) were also the toughest. It seems likely that the reverse is the case under normal growing conditions, but the etiolated light green grass was weakened by being placed under polythene. Thus, the initial preference of sheep for dark green grass was not fixed and may have switched either in response to the animals detecting the unreliability of the relationship between brightness and the nutritional content of the ryegrass, or to the variable toughness.

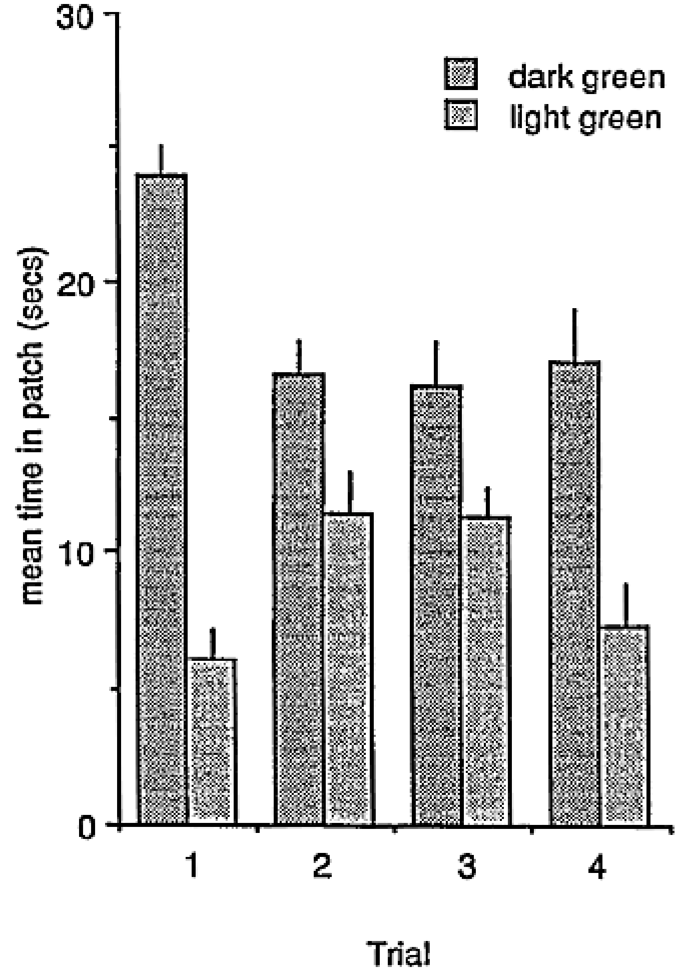


Figure 3.11. Time spent grazing by sheep (seconds) from dark green (▨) or light green (▨) trays of perennial ryegrass during 30 second trials, in which individual sheep had free access to both trays. Each sheep was tested over 4 consecutive trials. (Times spent grazing are mean; bars are standard errors; n = 15).

Table 3.12. Physical and chemical characteristics of Perennial ryegrass turves used in indoor colour choice trials, January 1986.

	Dark green (1)†			Dark green (2)††			Light green			one-way ANOVA
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	
Grass strength (grammes required to break grass)	172.0	12.9	20	-		-	132.5	10.5	20	$F_{1,38} = 5.6$*
Densitometer reading	1.18*	0.03	3	1.31*	0.01	3	0.81*	0.01	3	$F_{2,6} = 216.3$***
Water content (% fresh weight)	76.8*	0.2	10	83.2*	0.8	6	86.9*	0.3	5	$F_{2,18} = 124.7$***
Total nitrogen (% dry weight)	1.5*	0.003	10	4.2	0.7	6	3.1	0.1	5	$F_{2,18} = 42.8$***
Fibre content (% Modified Acid Detergent Fibre)	24.8	1.1	9	22.3	0.5	6	34.8*	0.6	5	$F_{2,17} = 32.1$***

†Turves left outdoors until January 1986 and fertilised with liquid fertiliser
††Turves brought into greenhouse in November 1985
*Significantly different from other groups at $p < 0.05$ based on Mean Significant Differences for unequal sample sizes (T-method, Sokal & Rohlf 1981).

3.5 Discussion

In the experiments described in section 3.2, sheep preferred to graze in dark green patches regardless of height, and in tall patches of ryegrass regardless of brightness. However, these preferences were not fixed, and they changed over a few days in the field experiments (section 3.2) and over very short time periods of minutes in indoor choice trials (section 3.4). As a result of grazing in dark green patches in field experiments the sheep increased the nitrogen content of their diet. In the following discussion the mechanisms that may account for these observations are considered, with particular emphasis on the role of visual cues.

The importance of visual versus olfactory cues in diet selection

There is an implicit assumption in the title of this chapter that sheep were using their sense of sight to respond to variation in the visual appearance of ryegrass swards. However, while cues used in diet selection, that are associated with the senses of taste and touch, can only operate while the sheep is biting, both olfactory and visual cues may operate over distance. I was unable to test whether sheep were using primarily vision or olfaction to locate and discriminate tall and dark green patches, because of the lack of time to investigate suitable controls. The relative importance of vision and olfaction in these experiments could have been investigated either by comparing intra-specific diet selection of sightless sheep with those having sight, or by comparing the behaviour of sheep with and without their sense of smell. Sight was found to be extremely difficult to manipulate in sheep (Tribe 1950a; Arnold 1966a). Blinded sheep did not behave normally and individuals took a great deal of time to become accustomed to blinkers (Arnold 1966a). Arnold (1966b) impaired the sense of smell in sheep by surgically removing their olfactory lobes. However, it may be possible to temporarily impair the sense of smell in a sheep by spraying a local anaesthetic into the nostrils, according to methods used by Chapple *et al.* (1987b). This method may be more viable than surgical impairment, in future experiments.

Although sheep may have been using olfactory cues to discriminate between perennial ryegrass swards varying in brightness as perceived by the human eye, evidence from other studies suggests that sheep were using primarily vision. In experiments testing visual discrimination in sheep, individuals were required to learn to associate a food reward with a brightness cue consisting of a dark or light card (C. V. Ensor & D. R. Bazely unpubl. data). Olfactory cues were completely controlled and could not have influenced the success of sheep in this task. The three sheep tested were 95-100% successful in associating the food reward with the correct brightness cue after two to three x 30 minute training sessions. In each session 25 choice trials were presented to a sheep. In experiments described in Chapter 4, sheep travelled between tall, dark green turves transplanted into a short, light green background sward. During one experiment, when these patches were >12 m apart, sheep 25 visited all patches, but rejected each of them after sniffing them for approximately 20 seconds. Rain had apparently washed dirt and paint onto them whilst they were stored next to a building before being transplanted into the sward. This also suggests that olfaction was not used to locate patches from a distance, since the sheep would not have visited the remaining patches after rejecting the first one if patches could have been distinguished by odour from a distance.

The exact role of the senses of smell and taste in diet selection in sheep still remains to be resolved (Arnold *et al.* 1980). Individuals deprived of the ability to smell and taste selected different diets from those in which these senses were unaffected, suggesting that smell and taste are used to discerminate between plant species (Arnold 1966b; Arnold *et al.* 1980). However, no significant difference in growth was found between groups of sheep with intact senses of smell and taste and those with impaired senses, leading Arnold (1966b) to conclude that these senses were not always critically involved in total intake of nutrients. The sense of smell does not apparently influence selection for different varieties of the same species (Tribe 1949; Arnold 1966b). However, as described above, smell may have been used by sheep 25 in rejecting a visually attractive patch of grass.

Brightness: visual cue to nitrogen content of perennial ryegrass

The total nitrogen content of background swards in paddocks was less than minimum levels required for maintenance of rumen microflora populations (Allden 1981; Simpson & Stobbs 1981; Van Soest 1982). Therefore, by feeding preferentially on dark green ryegrass patches, sheep increased their nitrogen intake to adequate levels. Experiments showed that brightness was a highly reliable cue to nitrogen and water soluble carbohydrate content of ryegrass. To my knowledge, there are no other studies of sheep grazing behaviour that have demonstrated an intra-specific diet preference related to variation in leaf brightness. However, this sort of preference has been demonstrated for insects. Myers (1985) showed that Cabbage White butterflies (*Pieris rapae*) preferred to oviposit on darker green cabbage plants (*Brassica oleracea* L.), which were higher in nitrogen and phosphorus than lighter green plants. The butterflies were apparently using brightness or colour as a cue to plant quality over distance (Myers 1985).

The role of sward height

As suggested by Black & Kenney (1984), sheep preferred to graze in tall patches. This preference was independent of brightness and nitrogen content: in section 3.2, the nitrogen content of tall patches was greater than the background sward in experiment 2, but in experiment 3 it was not. One reason why sheep may have preferred to graze in tall patches of vegetation was that they increased their overall rate of intake due to an increased bite size. Sheep grazing swards of 2.5 cm height had a bite size of <50 mg dry weight of plant material, compared with a bite size on swards of 15 cm height of about 150 mg (Black & Kenney 1984). Thus, intake rate increased with sward height, although it levelled off at around 10 cm sward height due to a decrease in bite rate and maintenance of a constant bite size on swards greater than 10 cm (Black & Kenney 1984). Additional evidence that sheep may prefer food which gives them an increased intake rate, comes from another series of experiments which demonstrated that the preference of sheep for dried forage, such as hay, increased when the forage was chopped to shorter lengths. Rates of dry matter intake increased as the same forage was chopped shorter (Kenney & Black 1984).

In experiments 1 - 3 (section 3.2), the tall patches of ryegrass were created by nutrient inputs from sheep urine and faeces. The preference of sheep for these patches was in direct contrast to observations of cattle avoiding tall, dark green patches in grass swards created in the same way (Plice 1951). This observation has lent support to the hypothesis that domestic ruminants prefer to graze in shorter vegetation. Plice (1951) suggested that these patches were avoided because the ratio of nitrogen and phosphorus to other nutrients was greater and lower respectively than that to which cattle were accustomed. When patches created by urination and defaecation were sprayed with sugar solution they immediately became highly acceptable and preferred (Plice 1951). Marten & Donker (1964) tested Plice's (1951) hypothesis, that tall patches were rejected because of their higher nitrogen and lower phosphorus content. In a nitrogen deficient paddock grazed by cattle they created control, tall, dark green patches by fertilising areas with phosphorus and nitrogen salts. At the end of an unspecified grazing period, up to 98% of 50 artificially created patches had been grazed, while 70% of those created by urination/defaecation had been partially consumed and 20% left completely untouched. Although they gave no indication of whether cattle actually preferred the artificially created patches relative to the low nitrogen background sward, or how the patches compared in physical characteristics or chemical content, their results suggested that some cue other than height and brightness was being used to discriminate between different types of tall, lush patches.

An alternative explanation for cattle avoiding tall patches created by urination and defaecation, is that by feeding in such patches, they increase the risk of infection by internal parasites such as nematodes. Artificially created patches may have differed visually from those created by defaecation in Marten & Donker's (1964) experiments due to parasite behaviour. The larvae of parasites such as the trichostrongyle nematodes, climb to the top of the grass sward and wriggle about, and this movement may have been perceived by the cattle (A. Keymer, B. Grenfell pers. comm.). Additionally, the artificial patches may have had a different odour that allowed them to be discriminated before being eaten. Spraying sugar solution onto such patches may either have washed off the parasites or destroyed the odour, thereby making patches acceptable to cattle - or even preferred, as Plice (1951) suggested.

It is unclear as to why, in my experiments, the behaviour of sheep differed so markedly from that of cattle. Perhaps the risk of re-infection by parasites was relatively low for sheep grazing on tall, naturally created patches, or the benefits outweighed the negative effects. I did not have any knowledge of the prevalence of parasites in my paddocks.

Sheep did not fully deplete tall patches in experiments 1 - 3 (section 3.2) or in section 2.3, Chapter 2. By the end of the experiments, these patches were still either taller than the background sward, or of similar height. In Chapter 4 I explore reasons why sheep leave patches before fully depleting them, even if they are preferred over the background sward. What is of interest in this discussion is the observation from experiments 2 & 3 (section 3.2) that the preference for height was not fixed. In 1985, sheep avoided the tall patches after four days, while in 1986, they started to graze them in proportion to their biomass. Thus, preferences could not have been based on height alone but on its association with some other cue or parameter, which must have changed, resulting in a switch in preference. It seems unlikely that these cues were visual or olfactory, since grazed and unacceptable tall patches were similar in appearance and presumably odour to grazed and still acceptable tall patches. In 1985, sheep may have been responding to the lower nitrogen content in the lower half of tall patches, although in 1986 there was no difference through the sward horizons. Another factor that may have influenced the switch in preference was increased toughness in tall patches as a result of biting into flowering culms and pseudostems present at higher densities in the lower sward horizons. Evans (1967a) demonstrated that leaf breaking strength was greater near the base of ryegrass leaves than towards the apex or tip. Although he did not test the breaking strength of pseudostems or flowering culms, it is reasonable to assume that these stiffer, supportive portions of the grass plant also have a high breaking strength. Liveweight gains of sheep were greater when they grazed ryegrass swards of lower toughness/ breaking strength (Evans 1964; Rae *et al.* 1964). These data demonstrate the way in which leaf strength may affect sheep growth, and perhaps influence diet selection. Since no data were collected on toughness or leaf breaking strength in my field experiments, I was unable to relate preference to this variable. However, since cellulose content of perennial ryegrass was found to be closely correlated with leaf strength (Evans, 1967b), in future experiments it would be well worth analysing vegetation for cellulose content, thereby allowing toughness to be taken into account when seeking an explanation for sheep diet preferences.

In studies of sheep grazing in multi-species plant communities, tall patches were dominated by particular plant species (Bakker *et al.* 1983; Grant *et al.* 1985). In these circumstances, sheep may have used height as a cue to sites to be avoided. The plant species found in tall patches were not inedible or toxic, but rather, less preferred species, such as the grass, *Nardus stricta*. (Grant *et al.* 1985). It would be of interest to determine whether such species, which may have been of similar nutritional quality to preferred species, were much tougher, and whether rates of dry matter intake of sheep forced to feed from such patches were lower than for sheep feeding on preferred species.

Preferences of sheep were not however dictated solely by physical parameters of the sward which enabled them to increase their intake rate. The bite size in short, dark green patches would have been much lower than that in tall patches. In addition, in section 2.3, sheep 267 took as many bites in short, transplanted patches as in tall patches, even though intake was lower from the short patches, and the sheep were biting into pseudostem. Therefore, there is an interaction between physical and biochemical parameters in influencing preference. Thus, the use of observed intake of biomass alone as a guide to sheep grazing preferences may give misleading results, and this method should be used in conjunction with behavioural data measuring time spent grazing in different types of forage or numbers of bites taken.

Senses and cues used in multi-species plant communities

Brightness was a reliable cue to nitrogen and water soluble carbohydrate content within a ryegrass monoculture, but in a multi-species plant community its reliability must be expected to decline. Leaves of different plant species may overlap in brightness, yet have completely different chemical and nutritional characteristics. However, variation in brightness may still have relevance as a cue to nutritional quality if sheep are able to discriminate between plant species in some other way. Harper (1977) suggested that the shapes of plants may be recognized by herbivores, and sheep apparently distinguished between different clover polymorphisms by recognizing white leaf marks (Cahn & Harper 1976). It would be of interest to determine whether sheep are able to distinguish plant species on the basis of their general appearance. It might be possible to test this by showing slides of different plant species to sheep, in experimental set-ups similar to those used by Kendrick & Baldwin (1987), or by Pietrewicz & Kamil (1981) with Blue jays (*Cyanocitta cristata*). This would control for the influence of olfactory cues.

The role of colour vision is also of interest, although it has long been assumed to be unimportant in diet selection in sheep (Tribe & Gordon 1949; Fontenot & Blaser 1965). In the introduction (section 3.1), I assumed that sheep are monochromats i.e. that they do not perceive variations in hue, and varying brightnesses are perceived as different shades of grey. However, the methods used by Tribe & Gordon (1949) to demonstrate the lack of colour vision in sheep contained various inconsistencies. As a result, an equally valid conclusion which may be drawn from their experiment is that sheep were unable to perform the behavioural discrimination task which they were set, while still possessing colour vision. Cones, which are the photoreceptor cells associated with colour vision (Jacobs 1981) have been found in sheep retinae (C. V. Ensor & D. R. Bazely unpubl. data). In addition, colour vision has been demonstrated in a variety of other ungulates (von Backhaus 1959). Thus, the question of whether sheep have and use colour vision remains unresolved.

Taste and odour may also be used by sheep to discriminate among plant species. Different plant species contain unique combinations of secondary compunds, many of which are aromatic or have distinctive tastes. Sheep have varying preferences for the the odour and taste of a variety of specific compounds present in plants, such as gramine and tannic acid (Arnold *et al.* 1980). Interestingly, preferences varied according to the concentration of the compound, but this was not related to concentrations present in plants (Arnold *et al.* 1980).

The role of learning

Thus far, I have discussed sensory mechanisms which sheep may have used to discriminate ryegrass patches varying in brightness and height, as well as functional explanations for observed preferences. However, what has not been discussed is how sheep may have had knowledge of the relationship between brightness and the nutritional content of ryegrass or that between height and the acceptibility of forage.

In past reviews of diet selection, it was often suggested that herbivores may have some kind of "euphagia" or nutritional wisdom that allows them to select forage on the basis of its nutritional content and toxicity (Tribe 1950a; Arnold & Dudzinski 1978; Arnold 1981). In general, little attention was payed to the sort of mechanisms that may have accounted for how this wisdom was gained (Zahorik & Houpt 1981). An early mechanism proposed was that animals have "specific hungers" for particular nutrients (Richter 1943 cited in Zahorik & Houpt 1981; Tribe 1950a). That is, they possess specialized receptors which allow them to detect the presence of a particular nutrient or poison in food. Individuals recognize specific deficiency states of nutrients, and are able to adjust their food intake to meet these requirements, as well as to avoid poisons (Zahorik & Houpt 1981). These "specific hungers" are innate and require no previous experience. While a specific hunger appears to exist for sodium intake in a variety of species, including sheep (Denton & Sabine 1963), it is unlikely that animals possess the great number of specialized receptors required to detect all necessary nutrients and possible toxins that may be encountered (Zahorik & Houpt 1981).

More recently, psychologists have examined the role of learning in diet selection (Zahorik & Houpt 1981; Shettleworth 1984). Broadly speaking, learning may be defined as any change in behaviour due to experience (Shettleworth 1984). Its role in diet selection involves the ability of animals to associate harmful consequences of ingesting particular food types with cues such as taste, odour or appearance, which characterize the food. After this learning period, the toxic foods are rejected. Learned food aversions have been most thoroughly studied in rats and this type of learning differs from traditional associative learning in that the cause of the illness is related to the effect even when the two events are separated by hours (Zahorik & Houpt 1981; Shettleworth 1984). Long-delay learning processes also result in rats increasing their preference for nutrient rich foods which bring about beneficial consequences i.e. recovery from nutritional deficiency symptoms (Zahorik & Houpt 1981).

Zahorik & Houpt (1981) have questioned whether the long-delay learning observed in rats is involved in diet selection in a wide variety of animal species. Herbivores, they argue, differ greatly from rats in their feeding behaviour. For example, they do not have discrete meals and ingest diets composed of many different plant species. Thus, it may be difficult to identify the diet item bringing about a specific harmful consequence. Zahorik & Houpt (1981, p. 310) stated that "the existing literature on the feeding behaviours and dietary dangers of large domestic herbivores offers little evidence that these animals' adaptive food preferences are the result of learning". Additionally, in ruminants, the rumen acts as a buffer between the animal and its meal and may delay the effect of a particular toxin even further (Thorhallsdottir *et al.* 1987), although a contrasting view is that the rumen may be beneficial in any long-delay learning process, because food cues may be reinstated through longer retention time of food (Zahorik & Haupt 1981).

Experimental results indicated that cattle, sheep, ponies and goats were able to learn to avoid a novel food paired with poisoning as long as the food was presented alone, and the consequences followed immediately after ingestion (Zahorik & Houpt 1981). Preliminary results from long-delay experiments indicated that for ponies, a separation time of 30 minutes between the ingestion of food and subsequent administration of poison, did not result in association of the illness with the food ingested. However, in mixed meal experiments, in which poisoning immediately followed the ingestion of novel foods presented with other familiar foods, the ponies learned to avoid the novel food (Zahorik & Houpt 1981). In another study, heifers learned to avoid alfalfa pellets when they were poisoned by intraruminal infusions of larkspur (*Delphinium barbeyi* L.) extract immediately after feeding (Olsen & Ralphs 1986).

Thorhallsdottir *et al.* (1987) studied learned food aversions in lambs and ewes, in which they were fed upon various types of food, some of which were mixed with lithium chloride. This poison is widely used in food aversion tests and causes diarrhoea and vomiting in humans and gastrointestinal disturbance and discomfort in sheep. Both ewes and lambs learned to avoid poisoned food pellets, and these aversions persisted even when they were again presented with the food two months later. After an experience with poisoning, sheep approached different novel foods cautiously and ingested only small amounts at first. Sodium chloride was used as a control for lithium chloride, because it also tastes salty but is non-toxic, and it did not result in learned aversions. Thus, in contrast to the findings reported by Zahorik & Haupt (1981), the sheep learned to associate poisoned food with gastrointestinal consequences which took effect up to two hours after ingestion. Interestingly, the sheep never completely stopped eating the poisonous food and always included a small amount in their diet (Thorhallsdottir *et al.* 1987). Consumption of some foods increased after a positive experience, demonstrating that foods which ceased to have harmful effects were also detected. The continued consumption of small amounts of food may be evidence of sampling by sheep, which Westoby (1974) suggested should be a feature of herbivore foraging behaviour. Herbivores must somehow keep track of a fluctuating environment, in which the nutritional value of different plant species and parts of plants is continually changing.

I can only speculate on the extent to which the preference of sheep for dark green and tall patches of ryegrass was the result of some learned association. If this was the case, then it seems likely that other non-visual cues were also associated with beneficial consequences. These additional cues e.g. ryegrass toughness, may have caused the switch in preference from tall patches to shorter swards and may also have caused the reduction in the preference for the dark green trays in indoor trials.

Alternatively, sheep may have some short term feedback system, akin to a specific hunger operating on a physiological basis, which allowed them to detect the nitrogen content of ryegrass immediately. Locusts (*Locusta migratoria*) are able to detect the protein concentration of artificial diets by a nutrient feedback mechanism which alters the sensitivity of maxillary palp gustatory receptors over very short time periods (Abisgold & Simpson 1987, 1988). To my knowledge, there is no research which has sought to determine whether an analogous mechanism exists in sheep. However, Arnold & Dudzinski (1978, p. 104) pointed out that the only taste signals from plants that may operate "are molecules which react chemically on receptors that transmit information" and that it is not possible for a sheep to recognize such parameters as nitrogen or crude fibre. Therefore, in investigations of diet selection in relation to chemical composition of plants, only molecular concentrations of specific chemical forms would seem to be of significance. (Arnold & Dudzinski 1978). Arnold & Dudzinski (1978) found that 14 different herbage characteristics were needed to explain 87% of preference variation in a principal component analysis of sheep diet selection. However, when they re-analysed data from Cowlishaw & Alder's (1960) study, they found that total organic acids present in forage e.g. shikimic acid accounted for 80% of preference variation. Organic acids were correlated with nitrogen content and they fit the criterion of being specific chemical forms. Thus, it appears that the role of organic acids in diet selection deserves further investigation as a potential candidate for the group of chemicals which may be used to assess nutrient quality on a short term basis.

It is apparent that a great deal of research still remains to be done on the mechanisms by which sheep and herbivores in general assess the nutritional and toxic qualities of the many plant species upon which they feed. Zahorik & Haupt (1981) believed that research into domestic herbivore diet selection has yielded little evidence of learning, but I would argue that most experiments have not been designed to detect its presence, and have only recently begun to address these types of questions (e.g. Olsen & Ralphs 1986; Chapple *et al.*

1987a, b; Thorhallsdottir *et al.* 1987). In indoor trials, the preference of sheep for dark green ryegrass was not maintained when the relationship between high nitrogen content and brightness was not consistent, and this demonstrated that an apparent visual preference in the field was highly changeable. It was entirely possible that a preference based on the association of visual cues with beneficial consequences was not maintained because sheep had learned to associate a multiplicity of cues (visual, olfactory etc.) with preferred forage. The rapidity with which unimpaired senses compensated for an impaired sense during learning periods in sheep was noted by Chapple *et al.* (1987b). The only two studies which have examined the possibility that long-delay learning may occur in large vertebrate herbivores have yielded apparently contrasting results (Zahorik & Haupt 1981; Thorhallsdottir *et al.* 1987). As Shettleworth (1984) pointed out, there is much to be learned about the role of learning in behavioural ecology.

Chapter 4

An application of optimal foraging theory to grazing behaviour: the marginal value theorem

4.1 Introduction

Optimal foraging theory (OFT) assumes that natural selection has acted on the decision rules made by a foraging animal to allow it to perform as efficiently as possible (Krebs *et al.* 1983). It is important to emphasise that while there is a set of general assumptions in OFT which have been set out in Chapter 1, there is no one theory and OFT encompasses a variety of models which have sought to make predictions about the optimal behaviour of animals subject to particular sets of constraints and assuming particular currencies. The general assumptions and the foraging models have been reviewed in detail in many papers (e.g. Krebs *et al.* 1981; Krebs *et al.* 1983; Pyke 1984; Stephen & Krebs 1986; Kacelnik & Cuthill 1987) and the validity of the former and usefulness of the latter have also been called into question (Gray 1987). While I acknowledge the existence of the debate concerning these basic assumptions, I was not concerned with justifying the optimality approach in this thesis, and the interested reader is referred to the various review papers on the subject.

Stephens & Krebs (1986) suggested that the patch-use group of foraging models may provide a more useful approach to the study of diet selection by vertebrate herbivores than the prey selection models. This was because food items i.e. plants, encountered and eaten by herbivores are not discrete in the sense envisaged by the prey models (Stephens & Krebs 1986). The patch-use models ask how long an individual should stay foraging in a patch before leaving in order to maximize its gain of some currency with respect to constraints such as travel time between patches. There is only one study of which I am aware that has taken a patch-use approach to herbivory (Parker 1984). It examined the foraging behaviour of a grasshopper (*Hesperotettix viridis*), but it was not experimental (Parker 1984).

The general objective of the experiments in this chapter, was to determine whether the grazing behaviour of sheep in ryegrass monocultures was consistent with the predictions of the marginal value theorem (Charnov 1976). This model, described below, predicts the time that a forager seeking to maximise its intake rate should stay feeding in a patch subject to the constraints of travel time between patches and the form of the gain function which describes the cumulative gain from a patch. It was of interest to investigate this aspect of sheep foraging behaviour because the results of experiments described in Chapters 2 and 3 showed that while sheep clearly preferred particular types of ryegrass patches, these patches were never fully depleted during a first visit. Sheep repeatedly returned to preferred patches, but the basis of this behaviour was unclear.

A variety of visual and biochemical parameters characterising preferred ryegrass patches was identified (Chapter 3). These parameters provided information about how sheep apparently perceived environmental heterogeneity or patchiness on a much finer scale than that identified by Belovsky (1978) in his study of habitat use by moose (*Alces alces*). This is one of the few other studies that has taken an OFT approach to herbivory (Belovsky 1978).

The marginal value model

The following description is adapted from Krebs & McCleery (1984). The marginal value model assumes that prey are patchily distributed within a forager's environment, and that prey availability within a patch decreases as a result of foraging activity. Thus, once a forager has arrived in a patch, it acquires prey rapidly at first, but the rate of acquisition diminishes with time. Thus, the cumulative gain curve for this prey may be of the form shown in Figure 4.1a. This curve, known as the "gain function", is assumed to be fixed for a particular patch type i.e. it is a constraint that cannot be changed by the forager. The units of the gain function are those of the currency e.g. energy, assumed to be of importance to the forager although they may be gross food intake as in Figure 4.1a. Travel time between patches is also a constraint which cannot be changed by the forager.

In order to maximize the gain of the designated resource (E) over total foraging time (travel time + time spent in a patch: T), i.e. maximise the overall rate, the animal should follow the marginal value rule (Figure 4.1b). It should leave the patch at the point T_{opt} which gives the steepest slope of the line AB. This line must touch the gain curve and intersect the *x*-axis at the beginning of the travel time period, when the forager left the previous patch.

The consequence of increased travel time between patches is that the optimal time to stay in a patch (optimal patch residence time) increases (Figure 4.1c). That is, the longer travel time is, the lower the value, i.e. the rate of resource acquisition, of moving from a patch. If patches vary in quality, then the forager should stay in a patch until the gain rate reaches the average for the envrionment (Figure 4.1d).

The simplifying assumptions of the model are listed below, along with specific predictions:

"**Assumptions**

1. Each patch type is recognized instantaneously.
2. The travel time between patches is known by the predator [forager].
3. The gain curve is smooth, continuous and decelerating (but see Kacelnik *et al.* 1981; Kacelnik 1984).
4. Travel time between and searching within a patch have equal energy costs. If costs differ, corrections have to be made (Kacelnik & Houston 1984) . . . .

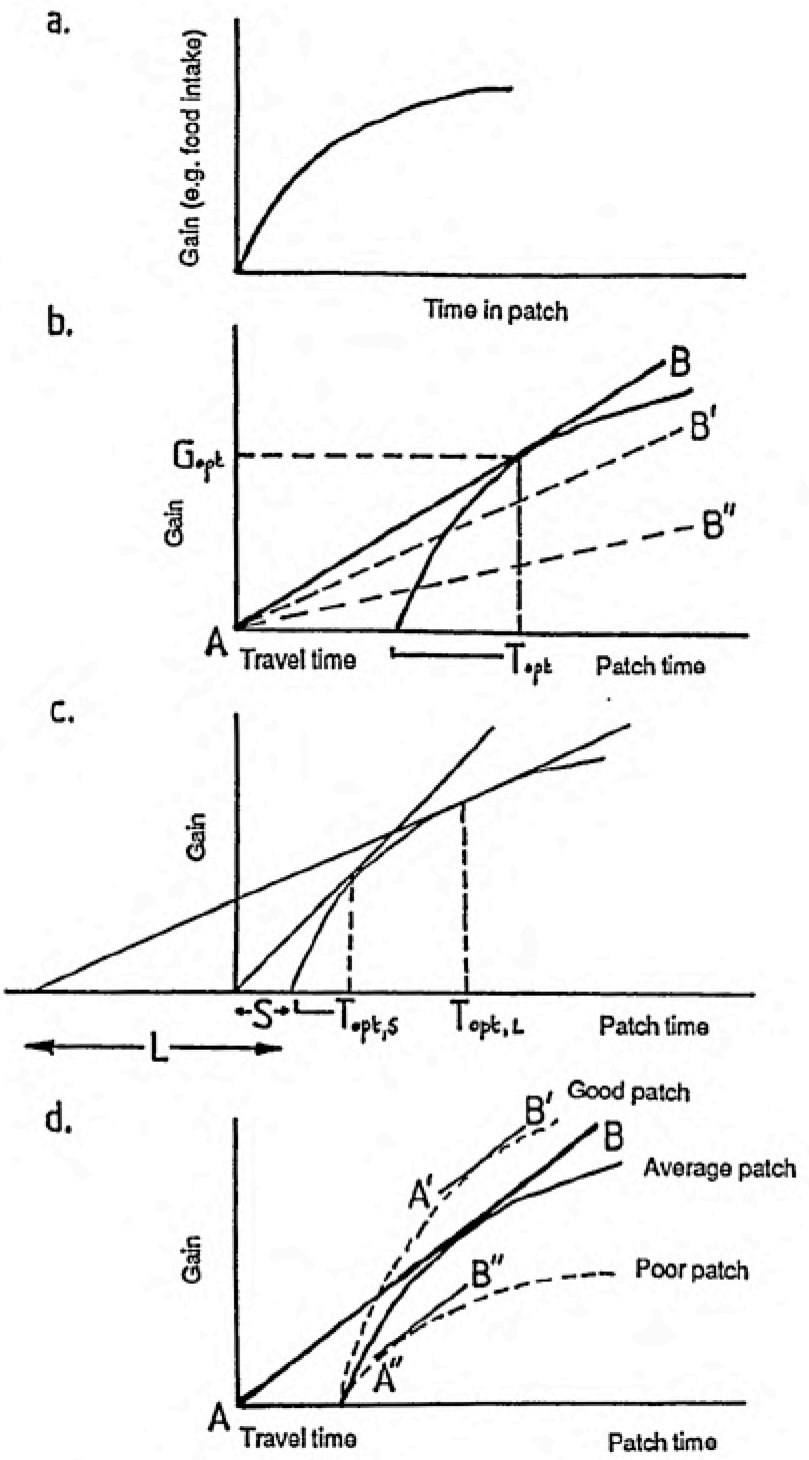


Figure 4.1. The marginal value model.

(a) An example of a gain curve arising from resource depression.

(b) The 'tangent' method of finding the optimal patch residence time T_{opt}. The rays (AB) from the origin have slopes E/T and the steepest feasible line is the solid one.

(c) As travel time increases, so does T_{opt}. For a short travel time (S), $T_{opt,S}$ is less than $T_{opt,L}$ for a long travel time (L).

(d) When there are several different patch types, each should be exploited until the gain drops to the average for the environment. From Krebs & McCleery (1984, p. 100).

Predictions

1. If travel time and the gain curve are known, then T_{opt} (Figure 4.1b) can be predicted.

2. If there is more than one patch type in an environment, all should be reduced to the same marginal gain rate.

3. If the gain curve is known, the relationship between T_{opt} and T_t [travel time] can be specified." (Krebs & McCleery 1984, p. 101).

The specific objective of these experiments was to determine the response of sheep to very good patches of ryegrass (from the sheep's point of view) transplanted into a much poorer ryegrass sward. The travel time between these good patches was manipulated and the subsequent patch residence times were observed.

4.2 Gain curves for sheep feeding on perennial ryegrass

4.2.1 Methods

Gain curves, as defined in the above discussion of the marginal value model, were determined for a total of 5 sheep grazing on swards of perennial ryegrass (*Lolium perenne* L.). The currency of the gain curves was defined as dry matter intake of perennial ryegrass. In 1986 the ryegrass variety "Melle" was used and in 1987 the variety used was "Parcour". The reason for this switch was that in grazing trials in 1986, the sheep appeared to prefer "Parcour". Three sheep, ewes number 224, 266 and 267, were used in 1986, and in 1987, two ewes, numbers 007 and 211, were tested. The gain curves were determined by feeding trays of *Lolium* to the ewes inside the sheep shed at Wytham Research Station, Oxford.

Trays (flats) of ryegrass were sown 2-2.5 months prior to being fed to sheep (Table 4.1). Regular size seed trays, 0.345 m x 0.21 m in area, were used. In 1986 1.2 g of seed were sown in each tray, and in 1987 1.5 g of seed were sown. During the growing period, each tray received approximately 10g of fertiliser (15.15.15 NPK Wiles Fertiliser) on one occasion, 10-14 days before the tray was used. During the periods in which each of the curves were determined, a minimum of three trays were trimmed to a uniform height of 11.5-12.0 cm in 1986 and 14.0 cm in 1987, and then harvested.

In order to compare the sward structure of trays used for gain curve determinations between years and between gain curve and field experiments the following measurements were made. All live biomass was removed by clipping with scissors at the soil surface. In 1986 the tiller density of each tray was determined with total counts for each replicate tray. In 1987, tiller density was estimated by counting out three sub-samples of 50 tillers from each replicate tray, taking their dry weights and comparing these with the total

Table 4.1. Planting schedule for trays of perennial ryegrass used for determination of gain curves.

Date of seed sowing	Date of intake curve determination	Age of trays
21 July 1986 1.2 g seed per tray	10-14 October 1986	80-84 days
21 August 1987 1.5 g seed per tray	22-24 October 1987	62-64 days

dry weight of live biomass for the tray. The mean pseudostem length and longest lamina length were estimated for each tray from the harvested vegetation. The live standing crop of each tray was then washed over a sieve and dried at 80°C before being weighed.

In addition to the trays used for characterizing structural sward parameters, in 1986, 48 other trays were planted and in 1987, a total of 30 trays were planted. Both sets of trays were planted on the same dates as the trays used for biomass and sward structure determinations. These trays were allocated to be fed to sheep. Before being fed to the sheep the ryegrass in the tray was trimmed to a pre-determined height equal to that of the trays from which all biomass was harvested (11.5-12 cm in 1986 and 14 cm in 1987). The pen set-up allowed the observer to tie down a tray of ryegrass in one pen while the sheep being tested was held in an adjacent pen (Figure 4.2). The sheep was then allowed to feed from the tray for a specified period of time, after which it was pushed away. The recovered tray was numbered and taken to the field laboratory where the remaining ryegrass biomass was removed by clipping, and was then washed and dried.

Thus, by weighing the vegetation remaining in the tray after the sheep had fed from it, and by subtracting this from the initial live standing crop of the tray at time 0 (known from the measurements of biomass from trays which had not been grazed), it was possible to determine the dry matter intake of the sheep for a particular time period. By combining a series of such dry matter intake points for feeding periods of different time lengths, a gain curve of dry matter with respect to time was generated.

The points for the gain curve for each sheep were determined in one day. Each sheep was allowed to feed from a total of 15-18 trays of ryegrass over a period of approximately six hours. Sheep fed from three trays for each specified time period. In 1986, intake from trays was measured after periods of 15 seconds, 30 seconds, 1, 2 and 4 minutes for sheep 266 and 224, and for sheep 267, measurements were made after 30 seconds, 1, 2, 3, 4 and 5 minutes. In 1987, live biomass remaining in trays was measured after 15 seconds, 30 seconds, 1, 1.5 and approximately 3 minutes. The feeding periods of different lengths were arranged in a random sequence e.g. 0:15, 1:00, 2:00, 0:30, 2:00 etc. The number of bites taken during each period was recorded, as was the total exposure time to each tray. Thus, a two minute feeding period included only the time spent by the ewe biting or chewing ryegrass removed from the tray. If the ewe became distracted or walked away from the tray, this time was excluded from the feeding period.

4.2.2 Results

In this section, the gain functions obtained for sheep grazing from trays of perennial ryegrass are

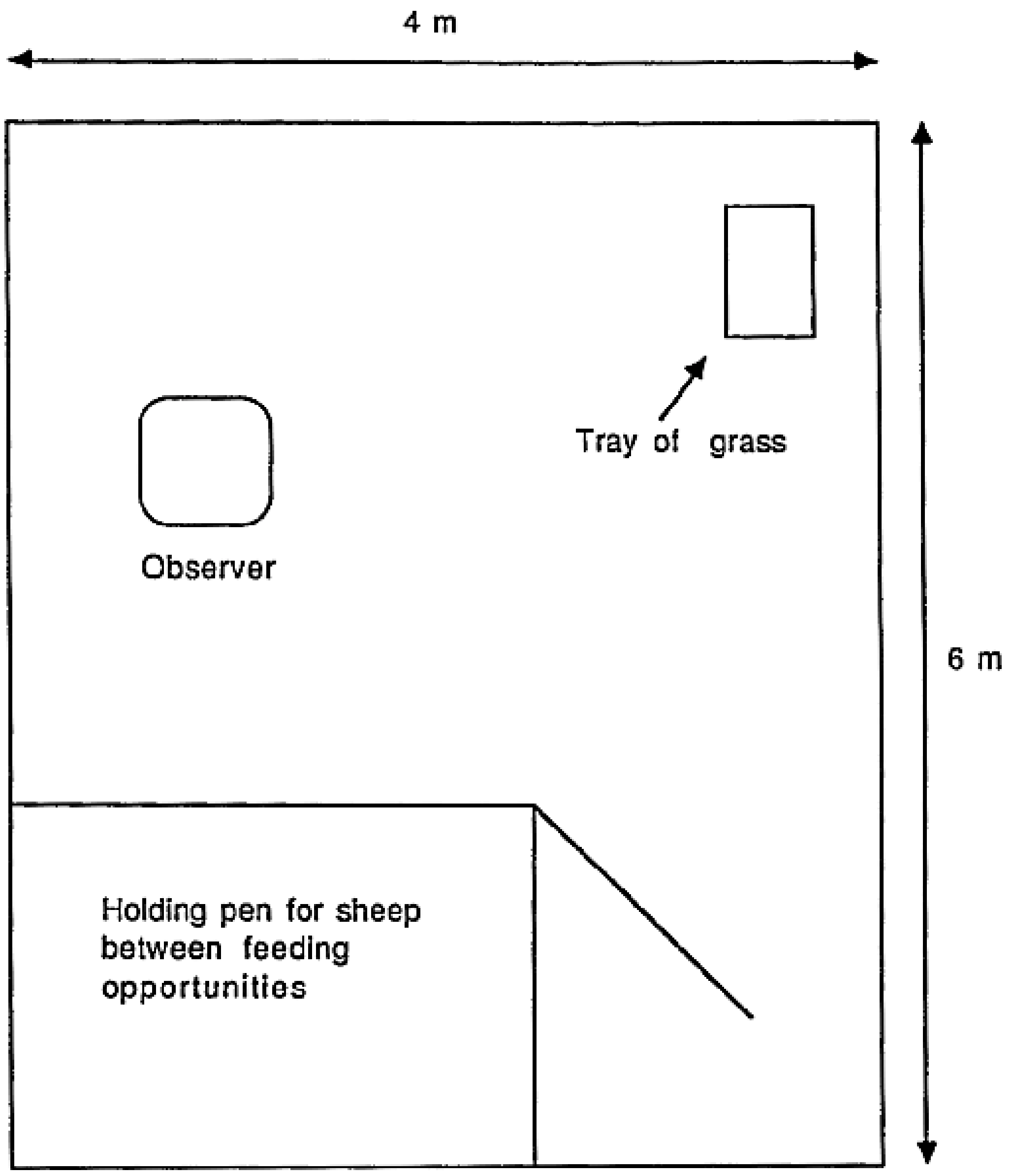


Figure 4.2. Arrangement of pens for determination of gain curves for sheep grazing on perennial ryegrass.

described, along with the structural characteristics of these turves. Structural sward characteristics were measured, because they provided a basis for determining the similarity of ryegrass patches used to define gain curves and those used in field experiments testing the predictions of the marginal value model.

The trays of ryegrass used for gain curves in 1986 and 1987 differed in their initial height and physical structure (Table 4.2). The live biomass in trays, which is expressed in the table as grammes dry weight metre^{-2}, did not differ between years. This was because the younger turves used in 1987 had a greater initial height of 14 cm compared with 11.5 - 12 cm, which compensated for their lower tiller density. This was also the reason for the greater lamina length in 1987. The tiller density was greater in 1986 than 1987 because of the longer growing period. This compensated for the initial lower sowing density of seed in 1986.

The cumulative dry matter intake for the five sheep measured in 1986 and 1987 increased with grazing time (Figure 4.3). Two functions, one linear and one exponential were fitted to these data. Although a straight line fitted by linear regression was significant for all sheep, the data were best described by negative exponential functions of the form

$$y = K_2 - K_2 e^{-K_1 x}.$$

The negative exponential functions determined for each gain curve are given in Figures 4.3a to 4.3e. Stepwise multiple regressions were used to compare the fit of linear regressions with negative exponential functions fitted with an iterative procedure. The variance remaining in the data after the linear regression model was fitted, was explained significantly by the exponential function, except in the case of sheep 266 (sheep 267: $F_{1,19} = 12.95^{**}$, sheep 266: $F_{1,16} = 3.7$ p=0.072 n.s., sheep 224: $F_{1,16} = 16.66^{***}$, sheep 007: $F_{1,16} = 96.30^{***}$, sheep 211: $F_{1,16} = 19.61^{***}$). The value for sheep 266 was, nonetheless, close to being significant. The stepwise multiple regression was then repeated, and the residual variance remaining after the exponential function had been fitted was tested against the linear regression model. Variance in cumulative gain versus grazing time explained by the exponential function first fitted to the data was highly significant and in no case was there significantly more variation explained by the linear model (sheep 267: $F_{1,19} = 0.21$ n.s., sheep 266: $F_{1,16} = 1.9$ n.s., sheep 224: $F_{1,16} = 1.62$, sheep 007: $F_{1,16} = 0.004$ n.s., , sheep 211: $F_{1,16} = 0.06$ n.s.).

Although it had been intended to determine gain curves for three sheep in 1987, sheep 25 refused to feed from the trays of ryegrass, in spite of being deprived of food for 1.5 days.

Gain curves differed between years in the time span that they covered. Sheep fed from grass trays for 4-5 minutes in 1986 and 2-2.5 minutes in 1987. This variation may have been partly due to the slight differences

Table 4.2. Structural characteristics and standing crop of trays of perennial ryegrass used for determining gain curves of grazing sheep.

YEAR	Live biomass (g dwt m^{-2})			Height of tray at time 0 (cm)	Tiller density (tillers m^{-2})		
	mean	SE	n		mean	SE	n
1986	307.1	29.4	3	11.5-12.0	20,633	784	3
1987	256.3	12.8	5	14.0	15,520	825	5
		t = 1.85 n.s.				t = 4.13**	

	Pseudostem length (mm)			Lamina length (mm)		
	mean	SE	n	mean	SE	n
1986	41.5	2.8	18	82.9	2.4	18
1987	32.1	1.9	50	108.1	2.4	50
		t = 2.65*			t = 5.95***	

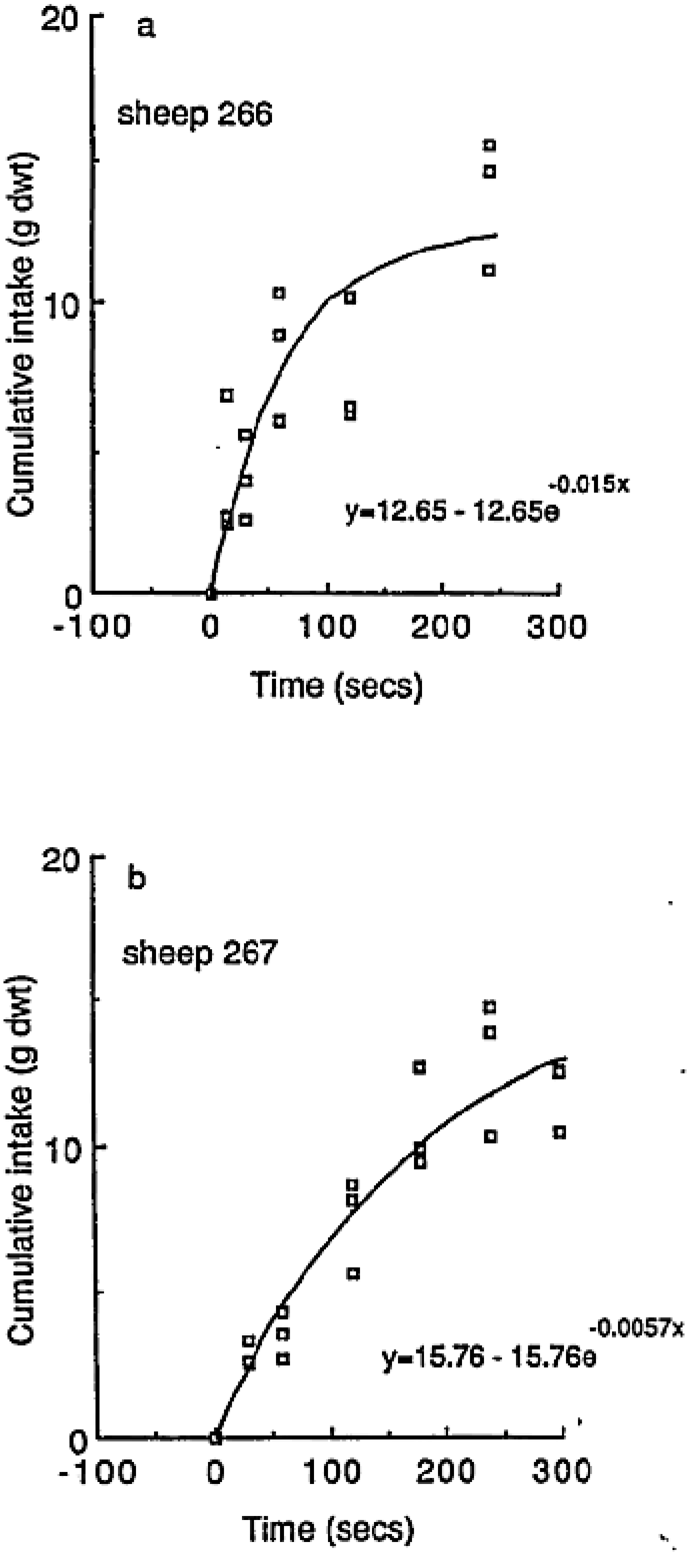
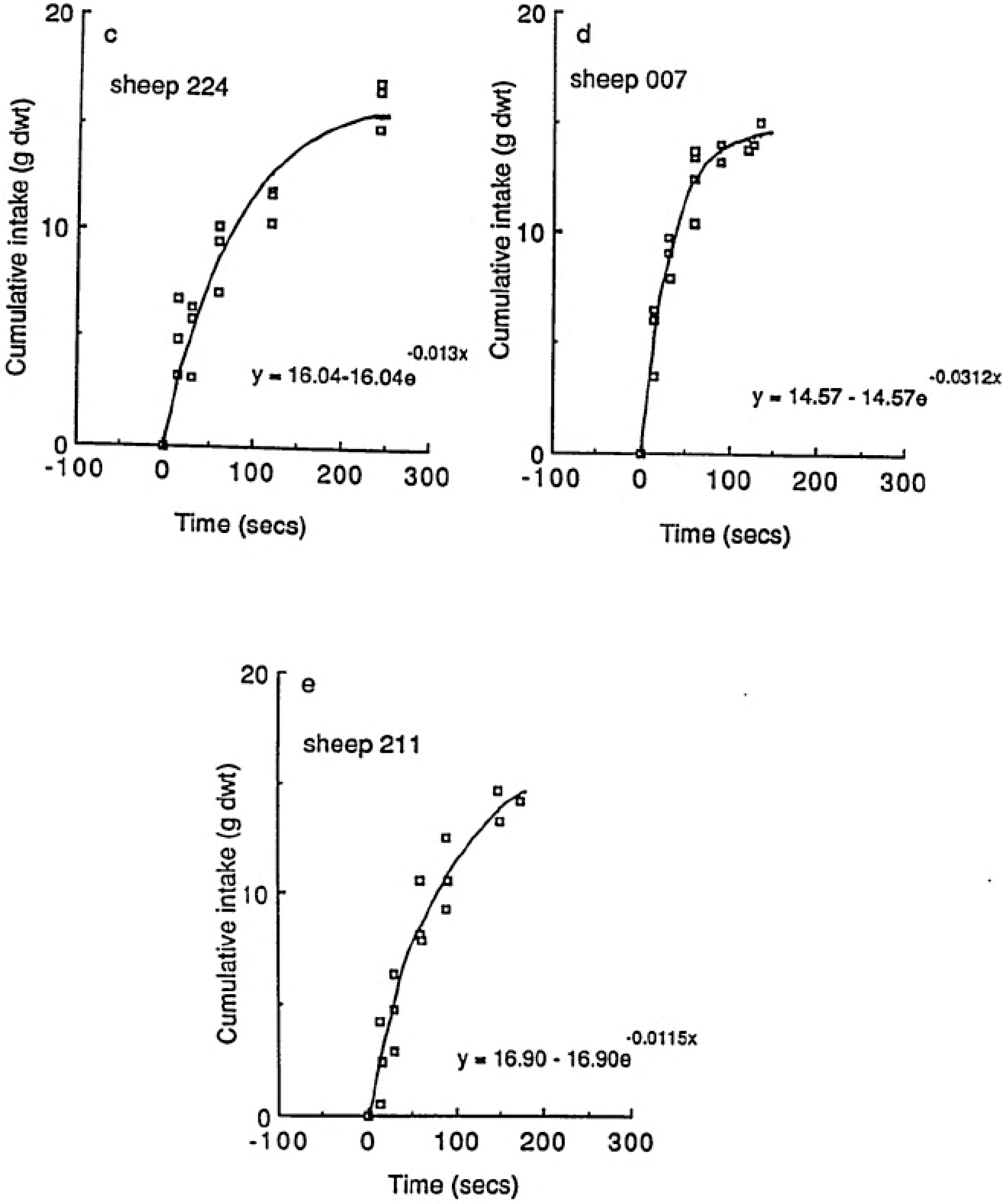


Figure 4.3. Gain curves measured as cumulative dry matter intake of biomass for sheep grazing from trays of perennial ryegrass. Gain curves were best described by functions of the form: $y = K_2 - K_2e^{-K_1x}$, denoted by the solid line in each figure.


c
sheep 224
Cumulative intake (g dwt)
20
10
0
-100
0
100
200
300
Time (secs)
y = 16.04-16.04e^-0.013x
d
sheep 007
Cumulative intake (g dwt)
20
10
0
-100
0
100
200
300
Time (secs)
y = 14.57 - 14.57e^-0.0312x
e
sheep 211
Cumulative intake (g dwt)
20
10
0
-100
0
100
200
300
Time (secs)
y = 16.90 - 16.90e^-0.0115x

in biomass at time zero. In 1986, initial biomass of each tray was 22.1 g dwt (307.1 g dwt m^{-2}). In 1987 it was 18.5 g dwt (256.3 g dwt m^{-2}). After four minutes in 1986, 60-73% of the total biomass on the tray was removed, while in 1987 up to 80% of the tray's biomass was removed by the sheep in just over two minutes. The ewes had great difficulty in grazing the remaining 20-40% of biomass on the tray once the sward height dropped to 2-4 cm. During the longest grazing periods the actual exposure time of the ewe to the grass tray was much greater than the grazing time. Gain curves were plotted against grazing time which included only time spent biting and chewing ryegrass removed from trays. Grazing periods greater than 2 minutes (1986), or 1.5 minutes (1987) constituted 30 - 60% of the total exposure time to the tray. After grazing continuously for 1-1.5 minutes, the ewe would look around and walk away from the tray in a loop and then return to it. Once the ryegrass had been depleted to a height of 5-6 cm, the ewe walked away from the tray for longer and longer periods before returning to graze more biomass. For shorter grazing periods between 90 - 100% of exposure time to the tray of ryegrass was spent grazing (biting and chewing).

The initial difference in biomass of trays between years did not completely account for the difference in time taken for maximum removal of biomass. The cumulative gain from trays was greater after two minutes in 1987 than in 1986. The probable explanation is that the higher tiller density in 1986 made sward penetration more difficult, while the greater amount of pseudostem relative to lamina, resulted in increased toughness. In combination, this would have resulted in a decreased rate of gain.

While the general shape of the curve that best fitted cumulative gain data for the five sheep was the same, the parameters K_1 and K_2 varied. The parameter K_1 represents the slope of the exponential function and the rate at which it drops. The value of K_2 is the asymptote that the exponential function reaches and represents the maximum biomass that it is possible for the sheep to remove. In theory, this could be the total biomass of ryegrass present on the tray, but in fact it was less.

The parameters K_1 and K_2 varied among sheep because aspects of grazing behaviour which determined cumulative gain of dry matter, such as bite rate, also varied. The mean bite rate, expressed as no. of bites min^{-1}, varied significantly among sheep for all grazing periods of greater than 15 seconds and less than 180-240 seconds when compared with Kruskal-Wallis tests (Table 4.3). Bite rates observed for each sheep over the periods of 15 seconds to 1 minute tended to be higher than those for longer grazing periods. The exception was sheep 267 which had the lowest overall bite rates, which did not vary with time.

Bite or mouthful size and its change with time was also calculated from the gain curve data. An alternative to the traditional method of calculating bite size by dividing the total cumulative gain over a four

Table 4.3. Bite rates (no. of bites min^{-1}) of sheep grazing from trays of perennial ryegrass for different periods of time.

	Grazing Period (seconds)											
	0-15		15-30		30-60		60-120		120-180		180-240	
Sheep	$\bar{x}$[†]	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
266	62.7	4.8	60.0	2.3	59.0	1.0	48.8	3.5	-	-	47.7	1.3
224	68.0	2.3	69.3	0.7	66.0	2.5	61.7	0.9	-	-	60.5	0.9
267	-	-	46.3	3.8	51.0	1.2	51.3	2.2	51.0	1.5	50.6	2.2
211	76.0	2.3	65.3	1.8	63.3	2.4	59.3	2.0	57.4	0.8	-	-
007	60.0	6.1	50.0	0	50.0	0.5	47.4	0.67	47.4	1.4	-	-
H[††]	6.36 n.s.		12.61*		13.13*		10.41*		6.49*		5.79 n.s.	

[†] n = 3 for each mean.

[††] H values are Kruskal-Wallis statistics comparing different sheep within the same grazing period. They are compared with χ^2 values at df = a - 1, where a = no. of groups (sheep) compared.

minute period for example, by the total number of bites observed. This new method is outlined in Appendix 4.1 (c f. calculations for bite size in Burlison & Hodgson (1985)). It is sensitive to changes in bite size which may occur over very short periods of time e.g. 1-4 minute periods.

It is apparent that for a sheep grazing from a particular patch (tray) of ryegrass, bite size drops rapidly with time (Figure 4.4). Mean bite size varied betwen 0.1 - 0.4 g dwt during the first 15 seconds of grazing. This tended to drop after another 15 seconds for all sheep except 267. After 1 minute of grazing time the mean bite size varied from 0.06 - 0.15 g dwt, after which time it dropped substantially for all sheep around 0.05 g dwt per bite. Bite size changed the least with time for sheep 267. This was consistent with her lower bite rate and cumulative gain curve with a lower initial slope than that for other sheep.

In summary, cumulative gain curves for sheep grazing from trays of ryegrass were best described by smooth, decelerating functions. There was among sheep variation in the parameters defining individual gain functions, as well as in other intake parameters such as bite rate and bite size. Bite size decreased rapidly as sheep grazed down through a ryegrass patch.

4.3 Effects of variation in travel time on patch residence time for sheep feeding on perennial ryegrass

4.3.1 Methods

In the following experiments the effects of travel time on patch residence time, or time spent grazing by sheep in a good ryegrass patch, were investigated. Travel time is assumed to be a constraint on foraging by the marginal value model.

4.3.1.1 1986 Experiments

In 1986 a group of three sheep was allowed to graze good patches of ryegrass transplanted into two adjoining paddocks. Each paddock was 25 m x 25 m, and the overall size was 25 m x 50 m. The sheep could move freely through the open gateways between the two paddocks. The paddocks were sown with perennial ryegrass in the spring of 1985. On two different days, the sheep were allowed to graze in two experimental designs which differed in the density of transplanted patches of ryegrass and thus in the distance between the patches (Figure 4.5). The sheep grazed in the high density experimental design on 3 September 1986 and in the low density design on 5 September 1986.

On the day preceeding each experimental day, the sheep were excluded from the two adjoining paddocks.

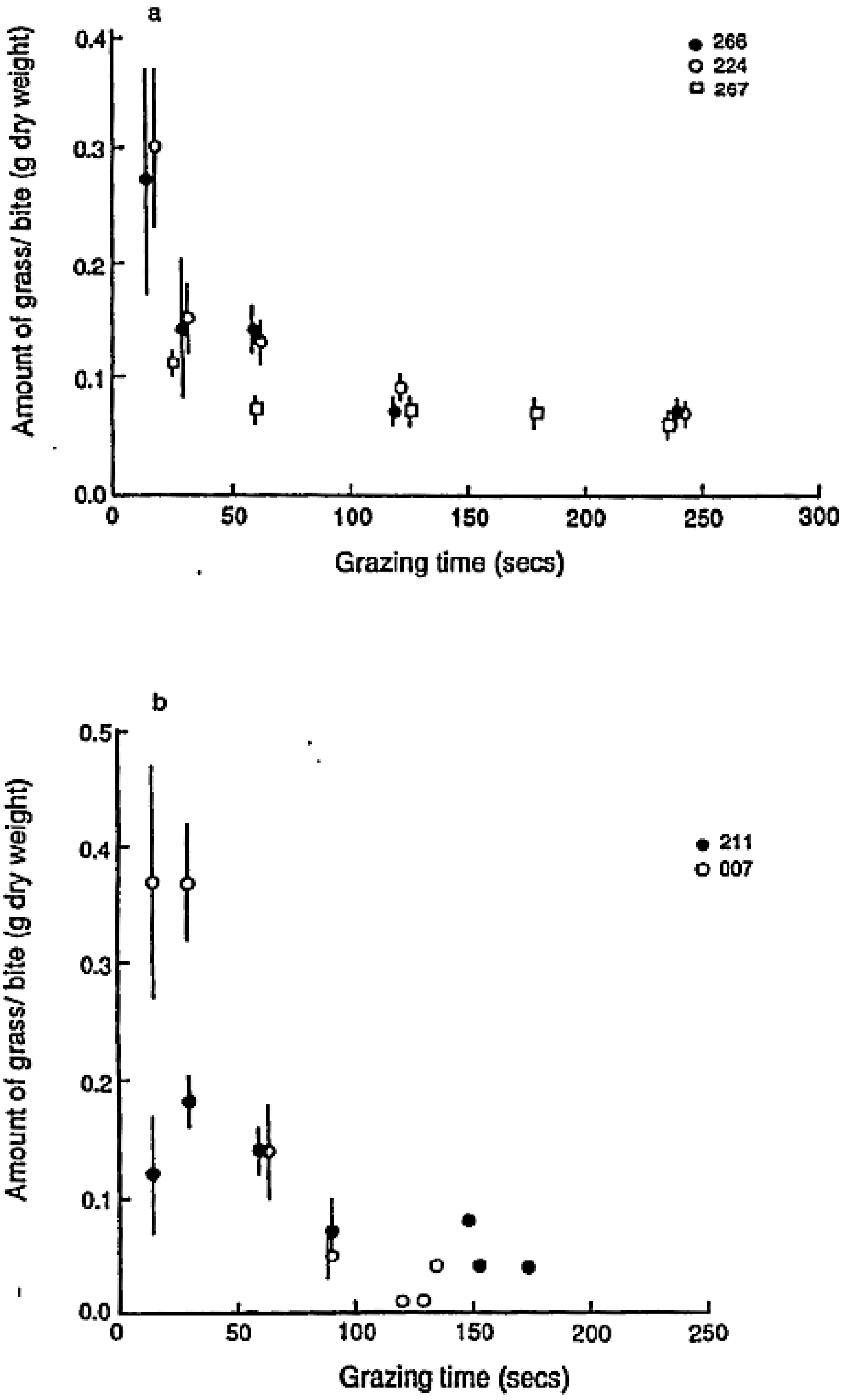


Figure 4.4. Change in bite size (g dwt) for sheep grazing from trays of perennial ryegrass.

(a) Sheep measured in 1986. (● 266; ○ 224; □ 267).

(b) Sheep measured in 1987. (● 211; ○ 007).

(Bite sizes are means ± S.E.; n = 3, or for points without error bars, n = 1.)

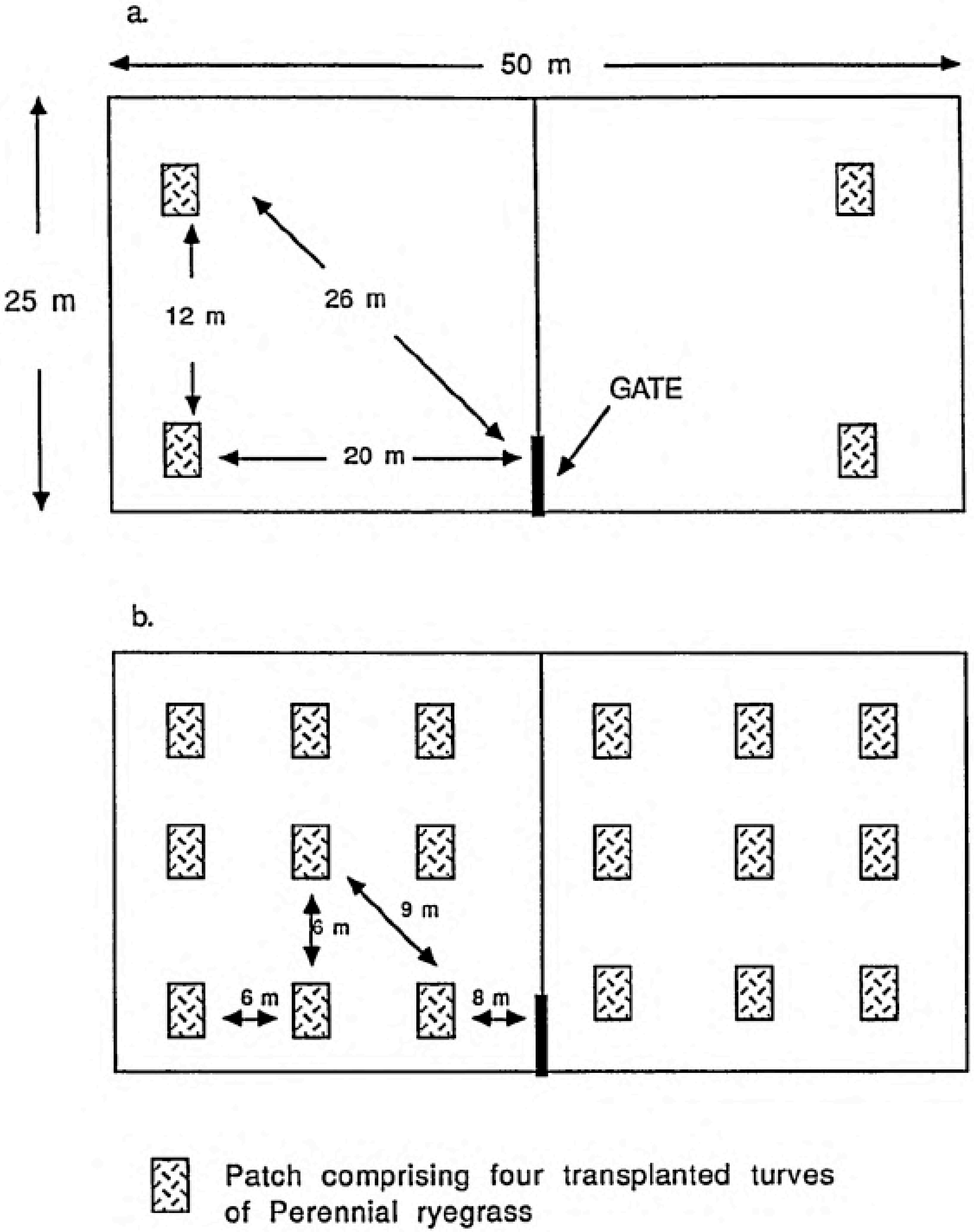


Figure 4.5. Diagram of two paddocks sown with perennial ryegrass showing transplant locations of good patches, September 1986.

(a) Low density experimental design.

(b) High density experimental design.

The sward height of the paddocks was measured and the turves to be transplanted were trimmed to the mean height of the background sward. The turves were then arranged in shallow holes (approx. 5 cm deep) dug in the paddock. Each patch of ryegrass was 0.69 m x 0.42 m and consisted of four turves grown in regular size seed trays (0.345 m x 0.21 m). Each turf was held in place with two or three metal skewer tent pegs. The head of each peg sat flush with the soil surface of the turf. On 3 September, each turf was trimmed to an initial height of 11.5 cm before being transplanted. A total of 72 turves was used to form 18 patches. On 5 September the initial height was 10.0 cm and 16 turves gave rise to four patches. The reason for this change was that between experimental days and also during the experiment the three sheep grazed down the background sward so that its mean height declined. The initial patch heights were adjusted so that the visibility of the transplanted turves in the background sward did not differ between days. Details of the ages of transplanted turves are given in Table 4.4.

At 07:15 on the day of each grazing experiment, the three ewes were allowed into the paddocks. As they grazed, the length of each visit to a good, transplanted patch was recorded with a stopwatch for each sheep. The time taken to travel between the patches was also recorded. After two hours the experiment was terminated.

4.3.1.2 1987 Experiments

In 1987, a series of similar experiments was run but with major modifications incorporated into their design. Because of the difficulty involved in recording relevant information for three sheep, only one sheep at a time was placed in the experimental paddocks. This also removed the problem of interference between sheep as they grazed, which had previously influenced time spent grazing in the patches. The two other sheep were penned up in the paddocks for the duration of the experiment and they did not have access to the transplanted patches. Three ewes were tested: numbers 007, 25 and 211. Two of these sheep were the same individuals used in gain curve determinations in 1987.

Manipulation of travel time between good patches

During the experiments, the sheep had access to four 25 m x 25 m paddocks linked by a central gateway (Figure 4.6). The gates were removed during the experiment to allow completely free access to all paddocks. The travel time between transplanted patches of ryegrass was manipulated in two ways:

1. By varying the distance between good patches of ryegrass.

Table 4.4. Planting schedule for trays of perennial ryegrass used in field experiments in 1986 and 1987.

Date of field experiment	Date of sowing	Amount of seed sown	Age of transplant turves - days
1986			
3 September	9 July	1.2 g Melle/tray	56
5 September	9 July	"	58
1987			
28 July	15/16 June	1.5 g Parcour/tray	42
9 August	15/16 June	"	54
11 August	15/16 June	"	56
13 August	15/16 June	"	58
15 August	15/16 June	"	60
17 August	16/19 June	"	60
19 August	16/21 June	"	60
21 August	19 June/4 July	"	48/63
25 August	4 July	"	52
27 August	4 July	"	54
29 August	4 July	"	56
1 September	4 July	"	58
3 September	4 July	"	60
5 September	4 July	"	62
6 October	16 August	"	51
8 October	16 August	"	53
9 October	16 August	"	54
10 October	16 August	"	55
12 October	16 August	"	57
14 October	16 August	"	59

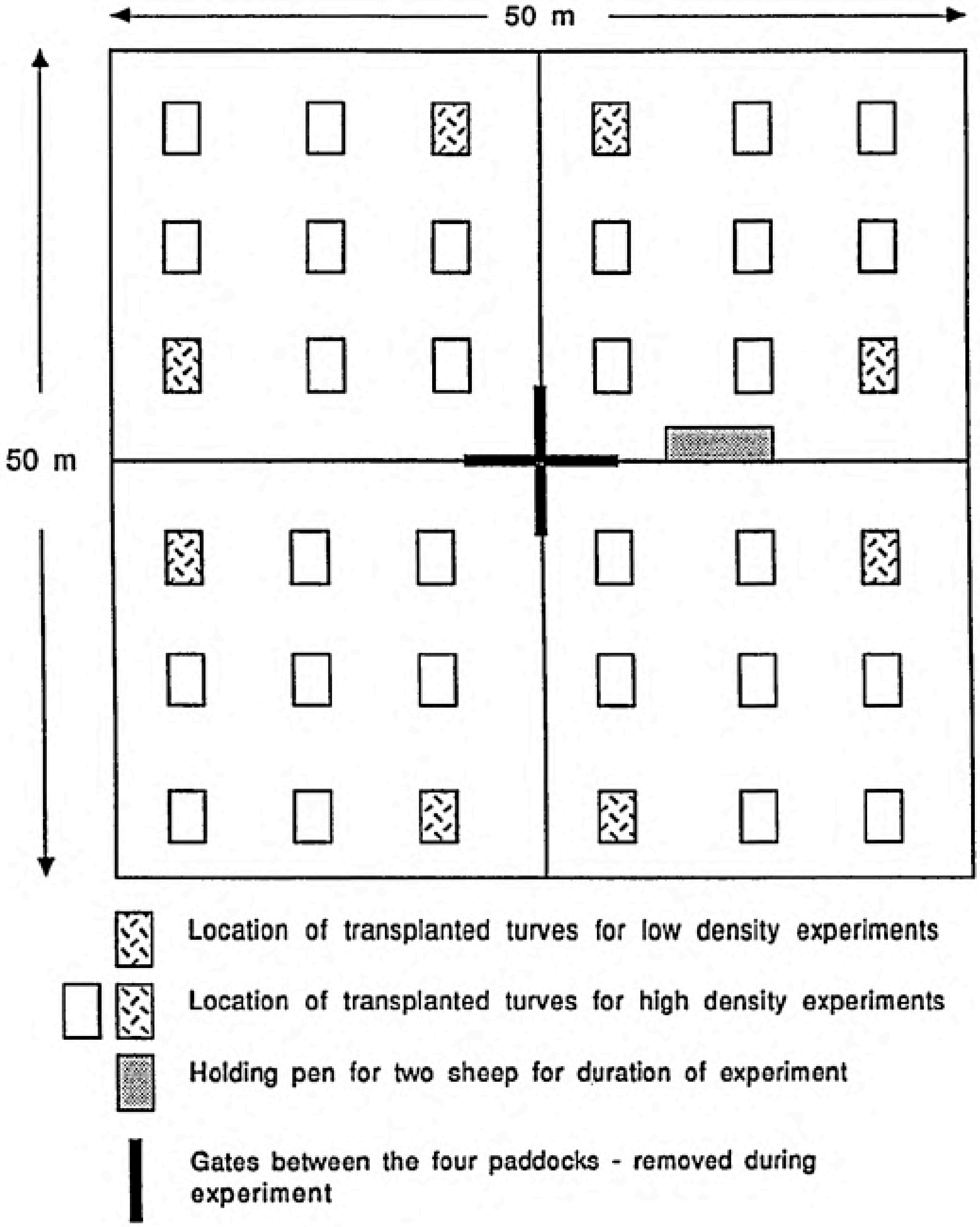


Figure 4.6. Diagram of four paddocks sown with perennial ryegrass showing transplant locations of good patches for high density (low travel time) and low density (high travel time) experimental days, August - October 1987.

2. By hobbling the sheep with "Ritchie" sheep hobbles.

These hobbles consisted of two strips of velcro approximately 20 cm long sewn together in the middle. One rough side was on the outside and the other rough side on the inside. Two of the hobbles were joined together before being fastened around a sheep's legs (Plate 4.1 a). When wound around the sheep's front legs, the two rough sides of Velcro came into contact with each other and fastened together (Plate 4.1b). By varying the distance between the sewing on the two hobbles it was possible to vary their effect on the sheep's movements.

In order to determine how the hobble affected movement, sheep were observed in detail on various occasions with and without the hobbles from July to September 1987. They were made to walk back and forth in the paddocks. The distances covered were measured as was the number of steps taken to cover the distance. The time taken was also measured. This timing took place when sheep were walking and not running i.e. two feet were always on the ground. I ensured that sheep were walking at the maximum speed possible when hobbled by measuring them as the walked towards a person holding a handful of dried food. When measuring unhobbled sheep, it was easy to discern the point at which fast walking became a canter.

Design of field experiments

There were four main experimental treatments used in 1987.

(1) An unhobbled sheep with eight patches.

(2) A hobbled sheep with eight patches.

(3) An unhobbled sheep with 36 patches.

(4) A hobbled sheep with 36 patches.

Each treatment was run on one day. The various treatment combinations and the dates on which they were run are given in Table 4.5. The sequence in which sheep were exposed to different treatments was randomized. This sequence was preceeded by a training session of one day for sheep 007 and 25. The purpose of this training session was to allow the sheep unhobbled access to the low density patch set up in order to learn that good patches were transplanted in holes in different paddocks. Very soon after the start of each experimental training-day, the sheep moved directly between the good, transplanted patches of ryegrass. They did not graze the background sward while good patches were available, and moved freely among the four paddocks. Thus, it took a very short time for a high preference to be developed for good patches. I decided that a training sesion was not necessary for sheep 211 which was penned up during experiments with sheep

Plate 4.1a. "Ritchie" sheep hobbles.

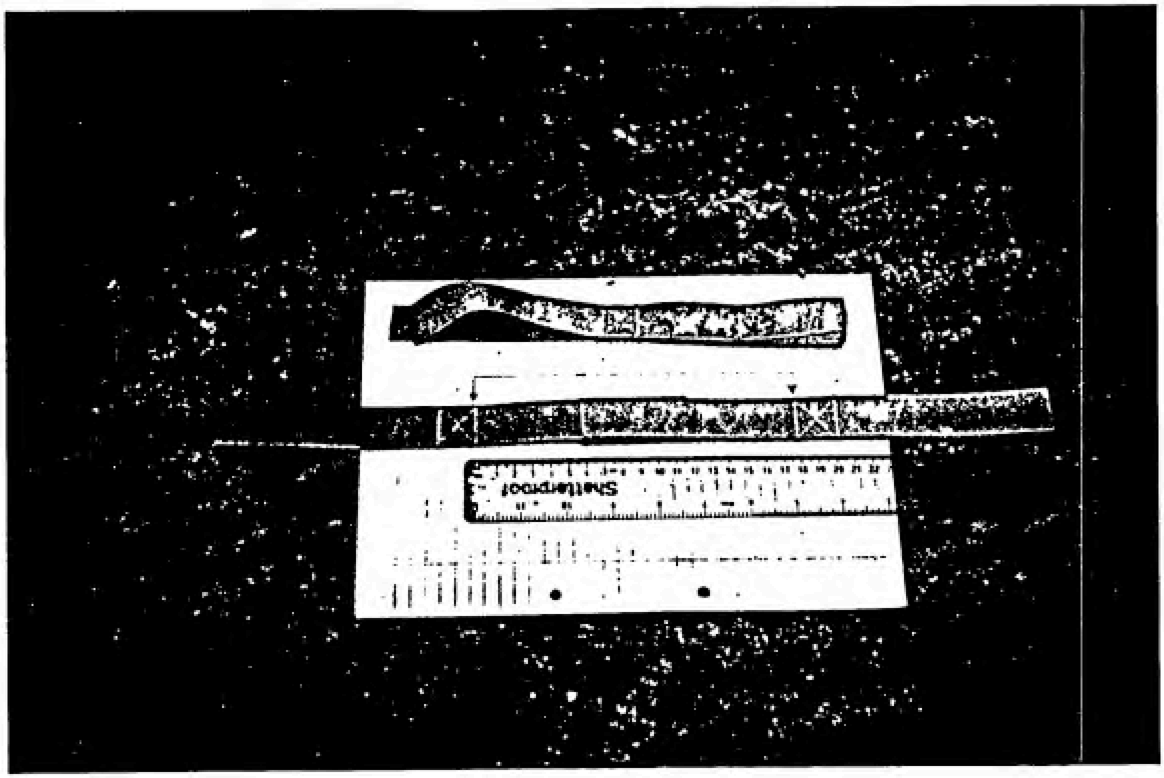


Plate 4.1b. Sheep 25 with hobbles in place.

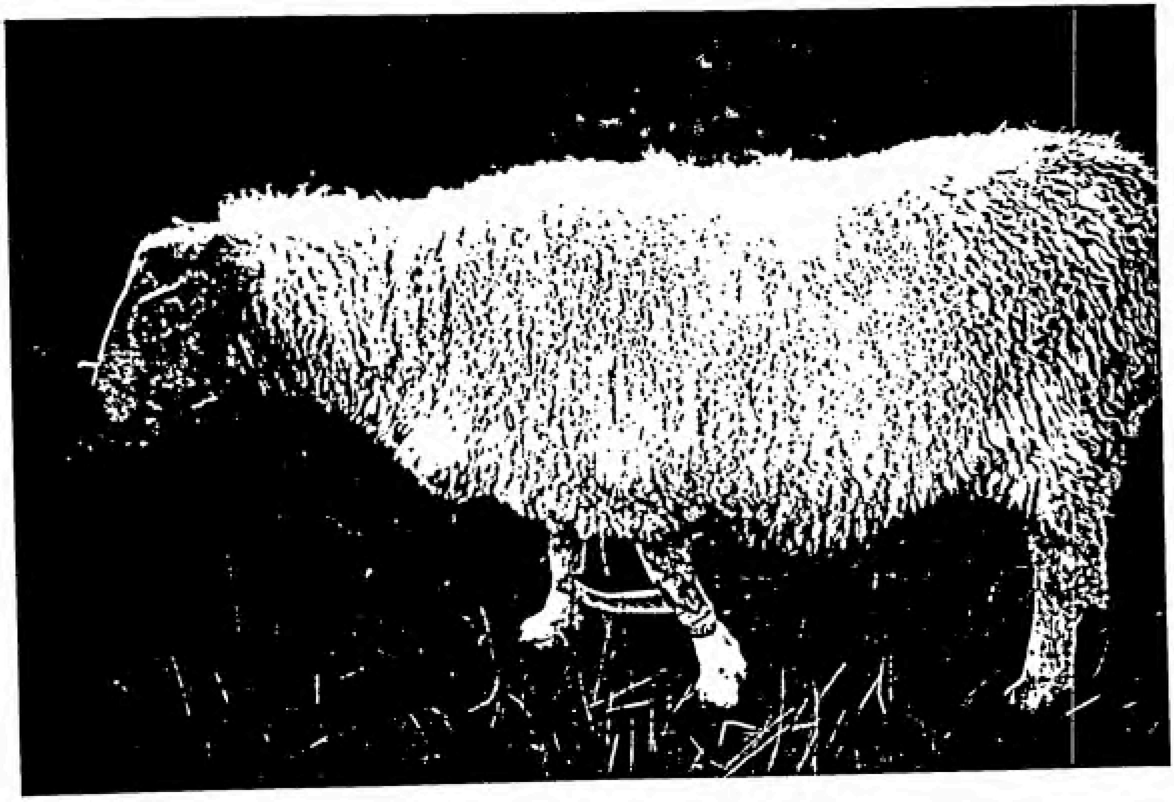


Table 4.5. Treatment combinations for field experiments, August-October 1987.

Date of field experiment	Sheep no.	Hobble used? Hobble length (cm)	Density and no. of patches
28 July[T]	007	No	Low (8)
9 August	007	Yes (26 cm)	High (36)
11 August	007	No	High (36)
13 August	007	Yes (16 cm)	Low (8)
15 August	007	Yes (26 cm)	Low (8)
17 August	007	Yes (16 cm)	High (36)
19 August	007	No	Low (8)
21 August	007	No	High (36)
25 August	007	Yes (13 cm)	Low (8)
27 August	007	Yes (15.5 cm)	High (36)
29 August[T]	25	No	Low (8)
1 September	25	Yes (16.5 cm)	Low (8)
3 September	25	Yes (16.5 cm)	High (36)
5 September	25	No	Low (8)
6 October	25	No	Low (8)
8 October	25	No	High (36)
9 October	211	No	Low (8)
10 October	211	No	High (36)
12 October	211	Yes (17 cm)	High (36)
14 October	211	Yes (17 cm)	Low (8)

[T] Training day during which the sheep became accustomed to the experimental procedure.

field experiments based on combining gain curves calculated in October 1986 with field observations of time spent grazing in patches would be less accurate than those made in 1987 (see section 4.2.2.).

Trays of ryegrass were fertilised with approximately 10g of fertiliser (15.15.15 NPK Wiles Fertiliser) on one occasion, 10-14 days before they were used. Structural characteristics of turves transplanted into the paddocks were measured in August and early October 1987 so that turves used in field experiments could be compared with those used for gain curve determinations. The background sward height of the four adjoining paddocks varied from 4 cm to 6 cm during the 2.5 months that the experiments were run. The three sheep were kept in these paddocks in order to keep them grazed down. Thus, the transplanted patches stood out clearly from the background.

4.3.2 Results

4.3.2.1 1986 Experiments

Results from 1986 are presented in Table 4.6. The mean travel time between patches was greater in the low patch density experiment when patches were further apart. The three ewes made more visits to a patch in the low density set-up, and the total number of bites taken per patch where all visits were recorded, was also greater. The mean time spent grazing in a patch on the first visit was 81.5 seconds in the low density experiment compared with 23.8 seconds in the high density set up. Since first visits to different patches were made by different sheep, these mean values include variation among sheep. Although I was able to note the sheep which first grazed in 5 out of the 18 patches on 5 September, I was unable to record patch residence times because another good patch was simultaneously being grazed for the first time by another sheep, and I collected data on that patch residence time. As a result, data from 5 out of 18 first visits to good patches was lost, and the sample size is n = 13 in Table 4.6. The sheep interfered with each other when grazing. A more dominant sheep would push a subordinate away from transplanted patches. Also, because the background sward was a similar height to the patches, the sheep did not graze exclusively in the good patches. This made the collection of travel time data difficult, because the sheep did not always travel directly between patches.

Because of the difficulty of determining travel times, it was not possibly to use gain curves determined in 1986 to predict optimal patch residence times and to then compare these with observed values. Also, I did not know how the gain curve measured for a patch consisting of one turf 0.21 x 0.345 m in area compared with that of a sheep grazing from a good patch consisting of four turves of that size.

Table 4.6. Effect of variation in travel time on time spent grazing by sheep in transplanted ryegrass patches (40 x 69 cm in size) on 3 and 5 September 1986.

	Low patch density (4 patches)		High patch density (18 patches)		
	mean	n	mean	n	
Initial patch height (cm)	9.8	24	11.3	108	
Travel time between patches (secs)	89.3	5	15.1	10	
No. visits per patch in 2 hrs	4.0	4	1.7	18	$F_{1,20} = 5.7^{*}$
Patch residence time on first visit (secs)	81.5	4	23.8	13	$F_{1,15} = 8.7^{*}$
Total no. of bites per patch in 2 hrs	186.8	4	89.6	15	$F_{1,15} = 9.5^{**}$

4.3.2.2 1987 Experiments

In the following three sections, the results of field experiments investigating the effect of manipulating travel times on time spent grazing in ryegrass patches are reported. In the fourth section, these results are compared with predicted residence times in ryegrass patches based on gain functions describing the cumulative dry matter intake from perennial ryegrass swards.

The effect of hobbling on grazing behaviour and travel time

Not enough data were collected to determine whether putting hobbles on sheep significantly affected the total amount of time spent grazing (Table 4.7). However, the 2-6% drop in the percentage of time spent grazing does appear to be very low. Therefore, it seemed likely that in experiments with good patches, the grazing behaviour of sheep would have been normal.

The following data illustrate the mechanisms by which hobbling of sheep decreased travel time. The primary effect of hobbling was that the step length of sheep dropped so that steps m^{-1} increased (Table 4.8). Data on steps m^{-1} were collected on more than one occasion for some hobble treatments, and where they were found not to be significantly different with one-way ANOVA comparisons, they were pooled. Multiple comparisons among pairs of means discussed below were based on minimum significant differences (M.S.D.s) calculated at $p < 0.05$, by the Tukey-Kramer method for unequal sample sizes (Sokal & Rohlf 1981). The effect on sheep 007 of a hobble of length 26.5 cm was not significantly different from the unhobbled treatment (M.S.D. = 0.289). Neither was the effect of 17 cm hobbles significantly different from that of 15.5 cm hobbles (M.S.D. = 0.289). However, these pairs of treatments differed significantly from each other and from the 13.5 cm hobble in their effect on steps m^{-1}. For sheep 25, the number of steps m^{-1} was significantly less without a hobble than with one, and this was also the case for sheep 211. Also, when comparisons of steps m^{-1} were made among sheep for the same hobble treatment, there were significant differences (No hobble: $F_{2,29} = 4.54^{*}$; 17 cm hobble $F_{2,27} = 11.06^{***}$).

Similar comparisons were made for measurements of the number of steps sec^{-1}. There was little variation among measurements taken on sheep 007 on three different dates for the no hobble and 17 cm hobble treatments. These data were therefore pooled. In the case of both sheep 007 and 211 hobbling had the effect of increasing the number of steps sec^{-1}. However, when the hobble was shortened to 13.5 cm, a critical length was reached and the although sheep 007 could walk it was obviously very difficult for her to manoeuvre her front legs. Two entirely different values for steps sec^{-1} were obtained for sheep 25 when

Table 4.7. Total time spent grazing by hobbled and unhobbled sheep.

Date and observation period	Sheep	Hobble?	No. of minutes spent grazing	% of total observation period
19 July 1987	3	Yes	137	32
09:10-16:14	007	No	144	34
	107	No	160	38
20 July 1987	3	No	142	43
09:05-14:35	007	Yes	131	40
	107	No	143	43

Table 4.8. Characteristics of movement of unhobbled and hobbled sheep.

Sheep	Hobble Length	Date	Steps metre^{-1}			Steps sec^{-1}			Speed m sec^{-1}
			mean	SE	n	mean	SE	n	
007	None	Pooled	2.65	0.05	19	2.34	0.04	24	0.88
	26.5 cm	9 Aug	2.77	0.09	7	-	-	-	-
	17 cm	Pooled	3.45	0.06	15	2.77	0.06	7	0.80
	15.5 cm	17 Oct	3.49	0.05	8	2.64	0.08	12	0.76
	13.5 cm	18 Aug	4.17	0.11	7	2.45	0.06	7	0.59
ANOVA on all hobble treatments:			$F_{4,55} = 80.2^{***}$			$F_{3,49} = 10.70^{***}$			
25	None	5 Sept[†]	-	-	-	1.91[††]	0.10	3	0.78
		17 Oct	2.45	0.08	7	2.52[††]	0.06	8	1.03
	17 cm	17 Oct	3.61	0.06	6	2.62	0.05	8	0.73
ANOVA on both hobble treatments:			$F_{1,12} = 114.9^{***}$			$F_{2,18} = 20.91^{***}$			
211	None (trotting)	17 Oct	-	-	-	3.58	0.17	6	
	None	Pooled	2.38	0.06	4	2.19	0.06	13	0.92
	17 cm	17 Oct	3.15	0.03	7	2.76	0.12	7	0.88
ANOVA on all hobble treatments:			$F_{1,10} = 166.6^{***}$			$F_{2,25} = 47.8^{***}$			

[†] These observations were made during an experiment.

[††] These two values for steps sec^{-1} were significantly different in the ANOVA (M.S.D. = 0.287 at $p = 0.05$). Therefore they were not pooled.

unhobbled on different dates, and while one value was significantly lower than that for the sheep with a 17 cm hobble (M.S.D. = 0.287), the other was not (M.S.D. = 0.212). This indicates that the base figure for steps sec^{-1} while a sheep is unhobbled can vary significantly. For comparison, sheep 211 was observed while walking and trotting or cantering. There was a highly significant difference between these two types of movement in the number of steps sec^{-1}. There was also significant variation among sheep in steps sec^{-1} when they were unhobbled (1-way ANOVA: $F_{2,44} = 7.71^{**}$), but when a 17 cm hobble was put on them, thre was no significant variation among sheep (1-way ANOVA: $F_{2,21} = 1.22$ n.s.).

An estimate of the speed of the sheep in m sec^{-1} was made by dividing the mean value for steps sec^{-1} by that for steps m^{-1} for a particular hobble treatment. It was not possible to assess variances etc. because in all cases the individual values for steps sec^{-1} and steps m^{-1} were determined separately and were not paired. The speed of each sheep declined with decreasing hobble length, but the amount by which it dropped differed among sheep. It was not possible to test whether the decreases were statistically significant. In some cases this difference amounted to 4-5 cm per second. Thus, it was apparently possible for the sheep to compensate to some extent for the decreased step length caused by the hobble by increasing step rate. Sheep 211 was apparently best able to maintain walking speed while hobbled.

In summary, hobbling resulted in an overall decrease in the walking speed of sheep, and a decreased step length.

Comparison of bite rates between field experiments and indoor determinations of gain functions

In addition to examining the effect that hobbles had on movement, it was also important to determine whether grazing behaviour affecting gain functions was comparable between field experiments and indoor gain curve determinations. When there was an additional observer, the number of bites taken from each patch was counted and bite rate was calculated (Table 4.9). There was considerable variation in bite rate. However, the range observed during five experimental days for two sheep fell well within that observed during the gain curve determinations (Table 4.3). Because the mean residence time or grazing period was known for each patch for a particular experiment day, the observed bite rate could be compared with that for the appropriate grazing period in Table 4.3. None of the bite rates observed in the field differed significantly for those observed during gain curve determinations for sheep 007 and 211.

Table 4.9. The mean bite rates of sheep while grazing in good patches. Sheep were observed during field experiments in August to October 1987.

Sheep	Date and Experiment Design	Bite rate (no. bites min^{-1}) mean	SE	n	Mean time spent grazing in patch (secs)	Comparison with gain curve bite rates†
007	9 Aug High patch density 26.5 cm hobble	44.0	3.2	15	46	t = 0.91 n.s. df = 17
	15 Aug Low patch density 26.5 cm hobble	46.1	3.5	6	65	t = 0.35 n.s. df = 7
	21 Aug High patch density No hobble	51.6	2.7	21	32	t = 0.29 n.s. df = 23
211	9 Oct Low patch density No hobble	54.9	1.5	6	88	t = 1.72 n.s. df = 7
	10 Oct High patch density No hobble	64.3	2.29	21	28	t = 0.17 n.s. df = 22

†t-tests compared bite rates (bites/min) of sheep grazing in transplanted patches with those of sheep grazing from turves used for the determination of intake curves (Table 4.3). The comparison was between the bite rate observed in the field with that observed during the grazing period equivelant to the mean residence time per patch during the field experiments.

The effect of manipulating travel time between good patches on patch residence time

The results of two experimental days were excluded from the following calculations. On 25 August, when the 13 cm hobble treatment was attempted, sheep 007 refused to move between the transplanted patches which suggests that some critical hobble length was reached at which movement became too uncomfortable. On 5 September 1987, sheep 25 refused to feed from any of the transplanted patches. She visited each patch during the experiment and spent 15-30 seconds sniffing each of them before leaving. The previous day white shade paint and dirt from a greenhouse near where they were stored had apparently washed into the turves.

The results for the remainder of the experiments are presented for each sheep in a separate table (Tables 4.10-4.12). In general, the time taken for ewes to visit the maximum number of patches was well below one hour. Thus, the cut-off criterion used for all experiments was the point at which approximately 60% of transplanted patches were visited. This varied from 6-7 patches on low patch density treatment days and from 17-22 patches for high patch density treatments. After the training day for sheep 007 and 25, once released into the paddocks from the small holding pen, they travelled directly between transplanted patches, which were 14 cm in height compared with the background sward height of 3-6 cm. No training was necessary for sheep 211 because she had much experience of visiting "used" transplanted patches after experiments were terminated, from August - September. At the end of each of the latter experiments I observed that she had a high preference for the remaining biomass in these good patches. Thus, I assumed that during the experiments with sheep 211, she would graze only in good patches and not in the background sward. This proved to be the case. During experiments the sheep did not always visit the nearest patch to the one that they had been grazing in when they were in a high density set-up. Instead, they often moved diagonally. Also they did not always visit each patch in a paddock before switching to another paddock. Their movement between paddocks was not inhibited by the relatively narrow open gateways.

In the high density patch set-up with 36 transplanted patches, the time taken to switch paddocks was excluded from the analysis. These times were 2-4 times greater than travel times between patches within a paddock. Paddock switches occurred three times at most during a 36 patch experiment, and accounted for 7-11% of the total number of observed trips between patches. Their inclusion in the analyses had a disproportionate effect on the mean travel time in experiments. Correlations between individual travel times between patches and the subsequent patch residence times were not significant for any experiments indicating that although travel between patches took longer when paddock switches occurred, the sheep was responding to some average travel time between patches that was much shorter (see Appendix 4.2 for correlation

Table 4.10. Results of experiments testing the effect of variation in travel time between good patches on patch residence time for sheep 007.

Date	Hobble Treatment	Travel time between patches (secs)			Patch residence time (secs)		
		mean	SE	n	mean	SE	n
Low Patch Density (8 patches)							
19 Aug	No hobble	26.7	4.3	7	50.8	8.3	6
15 Aug	Hobble 1 (26.5 cm)	34.6	4.3	10	64.8	11.9	7
13 Aug	Hobble 2 (16 cm)	58.9	9.8	6	82.2	8.2	6
High Patch Density (36 patches)							
11 Aug	No hobble	10.4	1.4	26	58.4	5.2	20
9 Aug	Hobble 1 (26.5 cm)	11.8	1.0	23	46.1	4.6	21
17 Aug	Hobble 2 (16 cm)	10.1	0.9	25	42.7	5.3	22
2-way ANOVA:	Hobble	$F_{2,91} = 18.2^{**}$			$F_{2,76} = 0.6$ n.s.		
	Patch density	$F_{1,91} = 180.3^{***}$			$F_{1,76} = 7.4^{**}$		
	Interaction	$F_{2,91} = 19.4^{**}$			$F_{2,76} = 4.7^{*}$		
High Patch Density (36 patches)							
21 Aug	No hobble	7.1	0.3	26	31.8	4.2	22
27 Aug	Hobble 2 (15.5 cm)	10.7	0.4	24	50.5	6.2	22

Data from 11 and 21 August were pooled as were data from 17 and 27 August and compared with the same hobble treatments run in low patch density experiments.

2-way ANOVA:	Hobble	$F_{1,110} = 71.9^{***}$	$F_{1,94} = 4.5^{*}$
	Patch density	$F_{1,110} = 277.0^{***}$	$F_{1,94} = 7.1^{**}$
	Interaction	$F_{1,110} = 57.3^{**}$	$F_{1,94} = 3.5$ n.s.

Table 4.11. Results of experiments testing the effect of variation in travel time between good patches on patch residence time for sheep 25.

		Travel time between patches (secs)			Patch residence time (secs)		
Date	Hobble Treatment	mean	SE	n	mean	SE	n
Low Patch Density (8 patches)							
6 Oct	No hobble	30.5	4.0	8	79.1	15.4	6
1 Sept	Hobble 1 (17 cm)	39.8	5.9	8	116.7	13.9	6
High Patch Density (36 patches)							
8 Oct	No hobble	7.5	0.3	24	25.8	3.6	22
3 Sept	Hobble 1 (17 cm)	10.7	0.4	26	46.8	6.2	21
2-way ANOVA:	Hobble	$F_{1,61} = 9.6^{**}$			$F_{1,51} = 11.7^{**}$		
	Patch density	$F_{1,61} = 166.6^{***}$			$F_{1,51} = 51.9^{***}$		
	Interaction	$F_{1,61} = 2.3$ n.s.			$F_{1,51} = 0.9$ n.s.		

Table 4.12. Results of experiments testing the effect of variation in travel time on residence time in ryegrass patches for sheep 211.

Date	Hobble Treatment	Travel time between patches (secs) mean	SE	n	Patch residence time (secs) mean	SE	n
Low Patch Density (8 patches)							
9 Oct	No hobble	26.6	5.7	6	87.8	5.76	6
14 Oct	Hobble 1 (17 cm)	30.9	5.2	8	75.0	4.91	6
High Patch Density (36 patches)							
10 Oct	No hobble	5.8	0.2	25	27.8	4.18	21
12 Oct	Hobble 1 (17 cm)	8.6	0.4	17	36.0	5.50	17
2-way ANOVA:	Hobble	$F_{1,52} = 2.6$ n.s.			$F_{1,46} = 0.1$ n.s.		
	Patch density	$F_{1,52} = 96.7$***			$F_{1,46} = 59.3$***		
	Interaction	$F_{1,52} = 0.1$ n.s.			$F_{1,46} = 2.7$ n.s.		

coefficients).

Travel times within and between paddocks were included in analyses of the eight patch experiments because paddock switches made up 50% of all trips between patches. Time taken to travel between patches within and between paddocks was much more similar in the eight patch experiments than the 36 patch experiments.

In calculating mean patch residence times i.e. time spent grazing in a transplanted patch, only the duration of a first visit to a patch was used. This was because while the gain function was known for patches when they had not been previously grazed, they were not known for revisited patches. The gain function from these patches which had a different initial biomass from that of newly transplanted replicates would have been been described by different values of K_1 and K_2. Sheep often visited patches more than once during an experiment allowing the collection of additional travel time data. This is why sample sizes for travel times were occasionally greater than those for patch residence times. Since consecutive patch residence times may have been interdependent, they were analysed for autocorrelation, and none was found (see Appendix 4.2 for results).

The effect of hobbles and patch density on mean travel times and patch residence times was analysed for each sheep with 2-way ANOVAs. Where necessary, data were log-transformed in order to meet homogeneity of variance criteria. In the case of sheep 007, one 2-way ANOVA was run to compare results for the high/low patch density treatments and the three levels of hobbling treatment run from 9-17 August 1987 (Table 4.10). A further analysis was carried out for hobble treatment (no hobble and 15.5 cm hobble) and day effect, for experiments run on the 11, 17, 21 and 27 August when this hobble treatment was repeated. The same hobble treatment did not differ significantly in its effect, when repeated (Effect of day on travel time: $F_{1,97} = 2.55$ n.s.; Effect of day on patch residence time: $F_{1,82} = 3.17$ n.s.). The data for different days (11, 21 August and 17, 27 August) were then pooled and compared with results of similar hobble treatments run in eight patch experiments, with a 2-way ANOVA on hobble treatments and patch density treatments.

When the distance between patches was increased (eight patch experiments compared with the 36 patch experiments) travel times increased (Tables 4.10-4.12). In all cases, the patch density treatment had a highly significant effect on travel time. In similar 2-way ANOVA comparisons, the patch density treatment had a highly significant effect on the mean time spent grazing in a patch by a sheep. In low patch density experiments, all sheep spent a greater amount of time grazing in transplanted patches compared with high density experiments.

The effect of the hobble treatments was similar. Within the low patch density experiments, hobbling a sheep increased her travel time between patches. Mean travel times varied from 26.6 to 58.9 seconds depending on hobble treatment and sheep. Travel times increased significantly when sheep 007 was hobbled and when the hobble length was decreased from 26.5 to 16 cm, travel time increased.

In the high patch density experiments, mean travel times were lower when the sheep were unhobbled and ranged from 5.8-10.4 seconds (Tables 4.10-4.12). When hobbled, the mean travel times of sheep varied from 8.6 - 11.8 seconds depending on sheep and hobble length. In 2-Way ANOVAS, the effects of hobbling on travel times were significant for sheep 007 and 25, but not for sheep 211.

When the travel times of sheep were slowed down as a result of being hobbled, the subsequent mean patch residence times in both the high and low patch density experiments were sigificantly greater overall compared with those for the unhobbled treatments for sheep 007 and 25. However, in the 2-way ANOVA involving three levels of hobble treatment for sheep 007, hobbling did not have a significant effect on patch residence time. Neither did it have a significant effect on the mean patch residence time of sheep 211.

Most of the interaction terms for 2-way ANOVAs run on sheep 25 were significant. This was primarily because the effect of the hobble on travel time and patch residence time was much greater in the context of the low density experiment than the high density experiment.

In general, travel times and patch residence times varied relatively little among sheep in the high density experimental designs. There was greater variation among sheep in the low density experiments which may have reflected differences in their ability to cope with hobbles and varying tendencies to walk more or less directly between patches spaced further apart. Also, smaller sample sizes necessitated by space limitations in the low patch density experiments may have contributed to this variation. Interestingly, sheep 211, was most able to compensate for the hobble in low and high density experiments and also in the tests run to examine the effect of hobbling on components of movement.

When the observed mean travel times were plotted against the mean patch residence times of different experimental days for each sheep (Figure 4.7), they were highly correlated (sheep 007: $r = 0.88^{**}$ $df = 6$; sheep 25: $r = 0.99^{**}$ $df = 2$; sheep 211: $r = 0.95^{*}$ $df = 2$). It was also possible to compare the mean number of bites taken per patch for some days (Table 4.13). The effects of patch density and hobble treatments were similar to similar to those observed for patch residence times. Sheep 007 took more bites $patch^{-1}$ in the low density experiment than in the high density experiment, and when hobbled, although these differences were not statistically significant. When sheep 211 was unhobbled, she took significantly more bites from patches

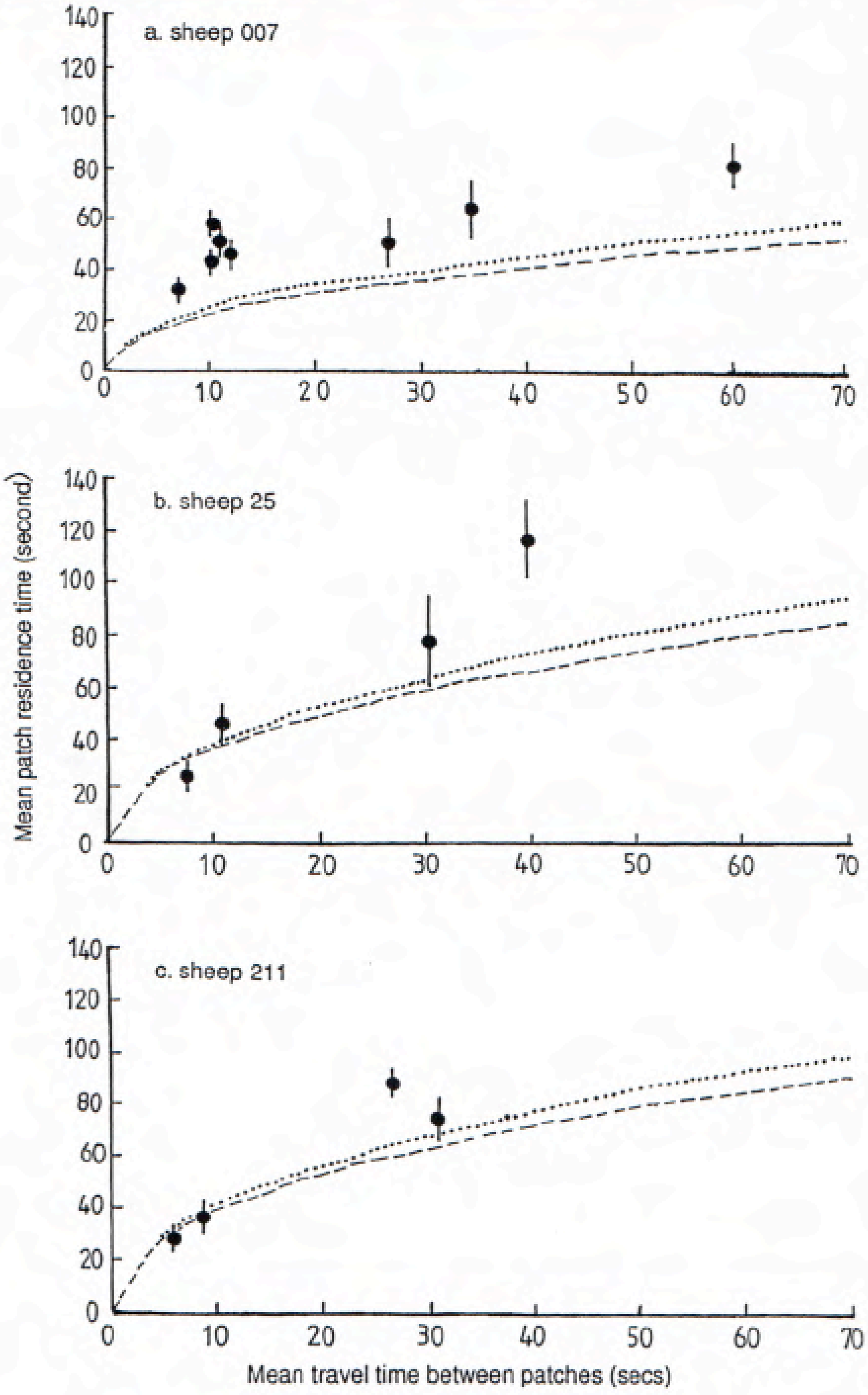


Figure 4.7. Mean patch residence times (seconds) plotted against mean travel times (seconds) between good transplanted patches.

(a) Sheep 007. (b) Sheep 25. (c) Sheep 211.

Dashed lines are predicted optimal patch residence times (T_{opt}) calcluated from gain curves in Figure 4.3. Dotted lines are predicted optimal patch residence times taking into account the difference in energetic cost between travel time (walking between good patches) and patch residence time (grazing within a patch).

(Each mean patch residence time is based on observations from a different experimental day. Sample sizes are given in Tables 4.10 - 4.12. Mean patch residence times (seconds) ± S.E.)

Table 4.13. The mean number of bites taken by sheep in each good patch in field experiments from August to October 1987. The following observations could be made when two observers were present.

Sheep	Date and Experiment Design	Bites/patch mean	SE	n	unpaired two sample t-test
007	9 Aug High patch density 26.5 cm hobble	32.4	3.4	21	t = 0.94 n.s.
	15 Aug Low patch density 26.5 cm hobble	39.7	8.5	6	
	21 Aug High patch density No hobble	24.7	3.2	21	t = 1.66 n.s.
211	9 Oct Low patch density No hobble	80.2	5.3	6	t = 6.05***
	10 Oct High patch density No hobble	28.0	4.3	21	

in the low density set-up compared with the high density set-up.

In summary, travel times and patch residence times increased with each other when good patches were located further apart and when sheep were hobbled. The effects of hobbling on travel times and patch residence times were not always significant, but there was a strong positive correlation between the average value per experiments of these two variables.

Predicted optimal patch residence times from gain functions

Optimal patch residence times were predicted for sheep 007 and 211 from gain curves generated in 1987, using observed mean travel times between patches. I assumed that gain functions observed in indoor trials could be extrapolated to field experiments, because the ryegrass turves transplanted into the paddocks for field experiments in 1987 were structurally similar to those of turves used for determination of gain curves for sheep 007 and 211 (Table 4.14). The difference in biomass per tray was not significant and the values for replicates varied from 17.4 g - 25.2 g for field experimental turves and from 16.3 g - 20.7 g for turves used for gain curves. In addition, observed bite rates of sheep were not significantly different in field and indoor trials (Table 4.9).

Since I did not obtain an gain curve for sheep 25, I used that for sheep 266, measured in 1986, since these sheep were of similar weights (74 kg). The biomass of ryegrass patches used in 1986 and 1987 for gain curve determinations was also similar, and I assumed that this was the main factor determining the gain function, although it may also be affected by individual variation and sheep and sward structure. An iterative solution was used to determine the optimal patch residence time as shown in Figure 4.1.

The optimal patch residence times for different travel times were also plotted in Figure 4.7. The observed patch residence times were compared with predicted times using one-sample t-tests in which the predicted time was taken as having no standard error. The observed times were 10 - 30 seconds greater than the predicted times for all points for sheep 007 and all but two observed points were significantly greater. Only one of four observed patch residence times were significantly greater than the predicted optimal times for sheep 211 and 25. These were patch residence times of 117 seconds for sheep 25 ($p < 0.05$) and 89 seconds for sheep 211 ($p < 0.01$).

Since the predicted optimal patch residence times were not in god overall agreement with observed times, the predicted optimal times were re-calculated to take into account any difference between the energetic costs of moving between good patches and standing and feeding from a good patch. From values taken from the

Table 4.14. Structural characteristics and standing crop of trays of perennial ryegrass used in field experiments August-October 1987. Statistics for t-tests refer to comparisons between parameters in this table and those for 1987 in Table 4.2.

YEAR	Live biomass (g dwt m^{-2})			Height of tray at time 0 (cm)	Tiller density (tillers m^{-2})		
	mean	SE	n		mean	SE	n
1987	302.9	16.9	8	13.0-14.0	17,805	1550	8
		t = 1.95 n.s.				t = 1.09 n.s.	
		d.f. = 11				d.f. = 11	

	Pseudostem length (mm)			Lamina length (mm)		
	mean	SE	n	mean	SE	n
1987	31.5	1.3	80	106.5	2.4	80
		t = 0.30 n.s.			t = 0.44 n.s.	
		d.f. = 128			d.f. = 128	

literature, I calculated the energetic cost to a sheep for standing and grazing in a patch to be 0.382 calories/ kg body weight/ sec, and that of travel time to be 0.840 calories/ kg body weight/ sec. The following values were combined to give these estimates: standing = 0.017 calories/ kg body weight/ sec (Osuji 1974); walking at a speed of about 0.8 m $\sec^{-1}$ = 0.60 calories/ kg body weight/ sec (Blaxter 1967); basal metabolic rate = 0.240 calories/ kg body weight/ sec based on a body size of about 70 kg (Blaxter 1967); eating fresh pasture = 0.125 calories/ kg body weight/ sec (Osuji 1974). The energetic values given for various activites are the energy required to do them over and above the basal metabolic rate. Thus, the energetic cost per unit time of travelling between patches was roughly twice that of grazing within a patch. I unable to assess whether there was an additional energetic cost of hobbling sheep above that caused by an animal being slowed down.

The additional time that a sheep was required to stay within a good patch in order to make up the difference in energetic cost was calculated from a gain curve converted from units of dry matter intake to caloric intake with the following equation:

Metabolisable energy (Megajoules/ kg dry matter) = 15.34 - 0.156 (% MADF) (Barber *et al.* 1984).

Since Modified Acid-Detergent Fibre content was known (see Table 3.11b), the metabolisable energy of perennial ryegrass was calculated to be 2,630 cals g dwt^{-1}. Using a similar iterative technique, a new series of T_{opt} values were calculated which took the differential energetic cost (0.458 calories/ kg body weight/ sec) between walking and standing and eating into account. These have also been plotted in Figure 4.7. While there was an increase in predicted optimal patch residence times, this did not result in a significantly better fit between observed and predicted values.

4.4 Discussion

When travel time between good patches of ryegrass was increased by two different methods, sheep responded by increasing their patch residence time. There was a significant positive correlation between average values of these two parameters. For both sheep 211 and 25, one of four observed patch residence times was significantly greater than the predicted optimal values. This occurred for mean travel times greater than 25 seconds. For sheep 007, nearly all observed patch residence times were significantly greater than predicted values. Thus, while the general positive relationship between travel time and optimal patch residence time predicted by the marginal value model was observed, a consistent agreement between observed and predicted patch residence times was not observed. Since I obtained only four data points for sheep 211 and 25, it was not possible to conclude categorically the model was successful in predicting sheep grazing behaviour for these two individuals. It was interesting that the significant differences between the observed and predicted values were consistently positive, suggesting that there may have been some specific explanation for these differences.

Stephens & Krebs (1986) discuss how the success of foraging models may be assessed. They point out that while much research has attempted to test predictions of the models, the assumptions of these models should also be considered, as should alternative hypotheses other than the null hypothesis of random choice (Stephens & Krebs 1986). In the following sections I discuss both the assumptions of the marginal value theorem and alternative explanations for the results.

How well were the assumptions of the marginal value model met?

In assessing explanations for the results, I have considered whether the assumptions of the marginal value model were met. These assumptions were listed in section 4.1. There was only one type of good ryegrass patch in these experiments, defined by results from previous experiments (Chapter 3). Patches were of taller, darker green ryegrass than the background sward. Sheep moved directly between them in all experiments, and never grazed from the shorter background sward. Thus, patches were apparently recognized instantaneously, which is the first assumption of the model. The training days and the free access of sheep to good patches left in place after each experiment allowed them to become familiarised with the locations of good patches and therefore with the travel times between them. Thus, it was likely that the second assumption of the model was met.

The cumulative gain curves from the patches, which were determined from indoor trials were best characterized by smooth, decelerating negative exponential functions. However, these functions, which formed the basis of the predicted optimal patch residence times did have confidence limits associated with them. These could not be defined, because the iterative method used to determine them did not allow these to be calculated although a method to do so is currently being developed by R. H. McCleery and A. Grafen. This error was not taken into account when determining the optimal patch residence times. An additional unknown was the extent to which these gain functions were fixed for a particular sheep. The model assumes that the gain function as well as the travel time is a fixed constraint. While I attempted to ensure that turves used in field experiments and indoor trials were replicates, it was possible that the behaviour of the sheep differed between these situations, so that gain functions were different. Thus, optimal patch residence times would have been different. The most likely method by which sheep might have varied the nature of the gain function, was by changing bite rate. However, bite rates measured in field experiments were not significantly different from those observed during gain curve determinations (Table 4.9).

These bite rates were in good agreeement with the range observed by Black & Kenney (1984), who reported rates of 40-50 bites min^{-1} on swards of 18 cm height and 50-70 bites min^{-1} on 10 cm tall swards. Only grazing time was included in these estimates. Penning (1986) measured bite rates with vibracorders so that total grazing time also included movement time around the fields, and found that at a sward height of 12 cm, the bite rate was approximately 40 bites min^{-1}.

The fourth assumption of the marginal value model was that travel between patches and searching within a patch have the same energy cost (Krebs & McCleery 1984). Sheep 007 may have remained in good patches for longer than predicted if the energetic costs of travel were greater than those of grazing in a patch, in order to compensate for this additional energy expenditure. This may also have been the case for sheep 211 and 25 on some experimental days when travel times were increased. During experiments with low patch densities, it was noticeable that, particularly when hobbled, sheep often slowed down or stopped when travelling between patches, and appeared to be resting. However, although I calculated that the energetic cost of travel was greater than that of staying in a patch, incorporation of this difference did not improve the fit between observed and predicted values for mean patch residence times. In aviary experiments with great tits (*Parus major*), which tested the predictions of the marginal value model, Cowie (1977) assumed that the energetic costs of travel and patch residence time were different. The observed residence times were greater than predicted values and after adjustments for differential energetic costs were made, the predicted and observed values for patch residence time were not statistically different (Cowie 1977). In this study, the gain curves were averaged for all six birds.

An additional explanation for the failure of the model to accurately predict patch residence times, relates to the definition of the currency being maximized. I have assumed that sheep were seeking to maximize their rate of dry matter intake. This was not necessarily the case, and the crucial parameter may have been some other nutrient such as nitrogen. However, since all good patches were similar and did not vary in their nutrient composition through their profile (see section 4.2, experiment 2), it was reasonable to assume that dry matter intake was directly correlated with nutrient gain. In addition, the results of Kenney & Black (1984), indicated that when nutritional parameters were similar and all choices equally available, sheep preferred forage which gave the greatest rate of dry matter intake. Had the nutrient content of good patches varied, then the problem of defining the relevant currency would have been much more critical. In Chapter 3, the sheep were found to prefer short, dark green ryegrass patches (higher in nitrogen) to tall patches. It was probable that the cumulative dry matter intake (gain functions) from the short patches were greatly different from the tall patch gain functions. Sheep could not have been maximizing dry matter gain by feeding as much as they did from the short patches. It would be interesting to conduct similar experiments to determine the response of sheep when presented with tall patches of varying nitrogen content. This would be a method of determining the currency of importance to sheep. The approach of comparing different currencies in different foraging models has been suggested as one way of providing alternative hypotheses to those provided by a specific foraging model and the null hypothesis (Stephens & Krebs 1986).

How sheep may know when to leave a good patch: rules of thumb

While the relationship between patch-leaving behaviour of sheep and travel time was predicted to some extent by the marginal value model, as pointed out by Krebs & McCleery (1984), the model does not account for how sheep achieved the observed result. Generally, it has been found that animals use various cues or "rules of thumb" to determine when to leave good patches (Krebs & McCleery 1984). One very simple rule may have been for sheep to base patch residence times on the proximity of the next good patch. Patches are seen and easily recognizable from a distance, and so a rule of thumb could be: "if a good patch is not close by then stay in the present patch for longer". However this would not have accounted for the effect of the hobble. Sheep may have been responding to the rapid change in bite size as each patch became depleted and learned to associate a particular bite size with a mean travel time between patches. The intial bite sizes measured during the first 15 seconds of the gain curve determinations were greater than those observed by Black & Kenney (1984) for similar sward heights, except for bite sizes measured for sheep 267 and 211 Bite sizes were 0.1 - 0.15 g dwt bite $^{-1}$ for sward heights of 18 cm and at 15 cm height, they were approximately 0.14 g g dwt bite $^{-1}$ (Black & Kenney 1984), which was similar to the values measured for the latter two sheep. Since Black & Kenney (1984) measured bite size over 30 second periods, it was surprising that their results were not in better agreement with values observed in this study. However, they tested only two sheep, and so this may have resulted in their failure to detect the variation in this parameter. They did not detect the rapid change in bite size as sheep graze in one location. An alternative "rule" that sheep might use to gauge when to leave a patch relates to grass toughness, which changes as a sheep bites down through a sward (Evans 1967a).

An alternative foraging model

While these experimental results have suggested that travel time was a constraint on sheep foraging behaviour, they do not conclusively demonstrate that sheep seek to maximize dry matter gain rates subject to this constraint. Taking account of the difference in energy costs between travel time and grazing within a patch did not explain the tendency of sheep to stay in good patches for longer than predicted. The area of research into "risk-sensitive foraging" provides some hypotheses as to why foragers may sometimes stay in patches for longer than predicted (Stephens & Krebs 1986). Here, I briefly discuss the notion of time discounting. As pointed out by Stephens & Krebs (1986, p. 147), "the major limitation of long-term rate maximizing is that it ignores the temporal pattern of energy intake: infinite energy gains tomorrow are irrelevant to an animal that will starve unless it finds another prey item before dusk." Extrapolated to sheep, this would mean that grazing ryegrass in a good patch in the present is of greater value than any intake that the sheep might obtain from a good patch in the future. This is because there is some uncertainty about the availability of good patches in the future. The value of being in a good patch in the present may be related to how hungry and animal is, and Stephens & Krebs (1986) describe the *z*-score model, which incorporates the effects of hunger and and considers time discounting. This model predicts that some situations, animals will stay in patches for longer than the optimal patch residence time.

Extending the predictions of the marginal value model to more realistic grazing situations

The foraging situation was highly artificial in two respects. First, all good patches were similar, whereas in other monocultures and multi-species plant communities, patches and travel times would be much more variable, and not so clearly defined from the human point of view. Second, sheep foraged as individuals in these experiments, whereas they normally graze in flocks. Thus, it is of interest to discuss how the marginal value model might be extended to make predictions about grazing behaviour in more complex, natural situations.

There are clearly problems with defining patchiness in more complex environments and Gray (1987) suggested that this is a major shortcoming of optimal foraging theory. However, although I designated good patches in this study, their specifications were based on parameters relevant to how sheep viewed heterogeneity in ryegrass monocultures. In multi-species plant communities, heterogeneity is often classified by describing the diversity of plant species. However, this does not take account of variation in the physical structure of the sward, which has been shown to influence grazing (reviewed in Hodgson 1982, see Chapter

1). An alternative method of assessing heterogeneity or patchiness from a sheep's point of view, rather than on a taxonomic basis, would be to examine step-bite data of the kind presented in Chapter 2. Had these data been collected in the Chapter 4 experiments, the nature of the patchiness would have been clearly defined by the sequences of consecutive steps and bites. However, these data were not collected as they did not have any bearing on the experimental results.

One might predict that the grazing behaviour of a sheep in a homogeneous sward would be characterized by few long sequences of steps between bites with step bouts consisting of half or single steps. This could be interpreted as the sheep viewing its environment as consisting of patches being adjacent or very close together, with a very short travel time between them achieved by a half or single step. In a more heterogeneous multi-species grazing environment, one might expect to observe longer bouts of bites between movements and greater numbers of bouts consisting of three or more steps, as sheep move between patches. These sorts of behaviour patterns were observed in sheep grazing on homogeneous grass re-seeds besides roads and rough heather moorland in Shetland (D. R. Bazely unpubl. data.). More realistic experiments could be based on these types of data. This approach to the characterization of the relative size of feeding areas is not new (cf. Thouless 1986), but to my knowledge has not been proposed as a means of extending tests of the predictions of the marginal value model to multi-species plant communities.

My experiments did not take account of the effect of social interactions among sheep. It seems likely that access to good patches will be influenced by a sheep's position in the dominance hierarchy, and this may influence predicted optimal patch residence times. In the experiments run in 1986 a group of three sheep were observed, and while mean patch residence times of first visits to patches were greater in low patch density experiments compared with high density experiments, it was not possible to predict the optimal patch residence times because of lack of accurate data on travel times. Thus, the effect of social interactions could not be assessed. However, I observed the displacement of sheep from good patches by other sheep, so it is likely that one effect might be that patch residence times would be shorter than predicted for subordinate individuals. The effect of social interactions may also provide an explanation for why sheep stayed in patches for longer than expected in 1987 experiments: they may have been unsure of whether their access to the next good patch would be prevented by another sheep, particularly when there was a low density of patches, and chosen to stay in their present good patch for longer. This explanation may be considered as a type of time discounting i.e. the sheep place higher value on being in a good patch because there is uncertainty about whether another individual is in the next good patch and is depleting it.

In summary, a highly simplified optimal foraging model, the marginal value theorem, was partially successful in predicting the amount of time that two out three sheep tested spent grazing in preferred ryegrass patches, although at high travel times, sheep spent more time in good patchs than predicted. A third sheep spent more time than expected in these patches but there was, nevertheless, the expected positive correlation between travel time and patch residence time. Although the energetic cost of travel was calculated to be greater than that of grazing in a patch, this did not account for why sheep tended spending more time in patches to compensate for this. Alternative models developed by researchers into risk-sensitive foraging provide hypotheses as to why foragers may stay in good patches longer than predicted. Travel time between patches appeared to be a constraint on grazing behaviour to which sheep responded. While the marginal value model appeared to be useful in making predictions about grazing behaviour in highly simplified environments, further experiments are required to assess the ability of these rules and constraints to predict grazing behaviour in more complex environments.

Chapter 5

Summary and Conclusions

Research into grazing behaviour and diet selection in domestic herbivores has followed an experimental approach for many years. However, from statements made in recent papers and reviews of this subject area, it is apparent that there is still a lack of understanding of many aspects of diet selection (Arnold & Dudzinski 1978; Arnold *et al.* 1980; Arnold 1981; Black & Kenney 1984). In this thesis, I have attempted to answer some of these unresolved questions.

5.1 Objectives of this study

In Chapter 1, I defined the following general objectives:

(1) To test experimentally whether sheep select forage of better nutritional quality when physical sward parameters (height, tiller density, pseudostem and lamina length) are held constant.

(2) To determine the response of grazing sheep to variation in the visual appearance and physical structure of perennial ryegrass (*Lolium perenne* L.) swards and to investigate visual cues associated with perennial ryegrass that sheep may use to assess its nutritional quality.

(3) To determine whether forage intake in grazing sheep can be predicted by a rate-maximizing model of optimal foraging theory.

5.2 Summary of results

(1) Sheep consistently responded to nutritional heterogeneity created in structurally homogeneous ryegrass monocultures. The nutritional criteria manipulated were nitrogen content and digestibility of ryegrass, because they are considered to be important nutrients for sheep (Freer 1981; Ørskov 1982; Van Soest 1982). Nutritional variation was created by transplanting fertilised turves of higher nitrogen content and digestibility relative to the background sward, into ryegrass paddocks. Sheep preferred to graze in these transplanted patches. They spent more time than expected grazing in them, and their intake from them was greater than from control patches of similar size created from the less nutritious background sward. Therefore, the "passive" selection hypothesis was discounted as a means by which sheep obtained more nutritious diets than the average available. This hypothesis explains the selection by grazers of more nutritious forage relative to the nutrient levels in available forage, as a consequence of the unselective grazing of the top layers

or horizons of vegetation, in which younger, more nutritious vegetation is concentrated (e.g. Alder & Minson 1963; Arnold *et al.* 1966; Hodgson 1982). Thus, grazers are viewed to some extent as "mowing machines". However, in my experiments, merely acting as a mowing machine would not have resulted in the selection of the most nutritious ryegrass available in the ryegrass sward.

(2) It has recently been shown that a variety of structural characteristics of ryegrass swards influence grazing behaviour and forage intake in sheep and cattle (reviewed in Hodgson 1982). However, there are few studies which have examined the effect of these characteristics e.g. sward height, tiller density, pseudostem length, on grazing preferences when animals are presented with a choice of sward types. Black & Kenney (1984) suggested that sheep may prefer to graze in taller swards because of the rate of forage intake from these swards is greater due to increased bite size, which is positively correlated with height. My experiments showed that sheep preferred to graze in tall ryegrass patches created by transplantation or *in situ*, which were either higher than or similar in nitrogen content relative to a shorter background sward. However, these preferences were not maintained in experiments which were run for more than six days in the same paddock, and sheep started to avoid tall patches in some cases.

In the same group of experiments, sheep showed even stronger preferences for grazing in short, high nitrogen patches of ryegrass of similar height to the background sward. This indicated that intra-specific diet preferences were not only influenced by structural sward parameters related to increased biomass intake, but also by nutritional content of ryegrass.

The brightness or amount of light reflected from ryegrass, i.e. whether it was dark or light green, was quantitatively related to the nitrogen and water soluble carbohydrate content of vegetation. In field experiments, the ryegrass patches which were high in nitrogen were also darker green relative to the background sward. It seems likely that sheep used brightness as a visual cue to locate the more nutritious patches of ryegrass when they were of similar height and structure to the background sward. However, it is probable that sheep also relied on other cues to assess nitrogen content of vegetation; in indoor choice trials in which the predictability of the relationship between brightness and nitrogen content of vegetation was not maintained, the preference of sheep for dark green trays was reduced. One possible physical sward parameter which may influence selection is toughness of vegetation. Increased toughness of tall patches as they were grazed down may have explained why sheep switched from preferring to avoiding tall patches.

Due to lack of time it was not possible to determine whether dark green patches were located primarily by sight, and approporiate control experiments in which the senses of sight and smell were alternatively impaired were not run. In addition, I was unable to run factorially designed experiment in which all combinations of brightness and height of swards were available. This type of experiment may have given a clearer indication of the way in which sheep ranked their preferences for height relative to brightness. Also, data on the relative toughness of ryegrass would have been useful, since it influence on diet choice was not known.

(3) A consistent observation made in the experiments described in Chapters 2 and 3 was that sheep did not deplete preferred patches on initial visits to them. These patches were continually revisited and regrazed during the experiments. The marginal value theorem, an intake rate-maximizing optimal foraging model, makes predictions about when a forager should leave a patch and provides an explanation for why sheep may leave preferred patches without fully depleting them. This model assumes that foragers are constrained by travel time between patches and by their gain function (intake curve) from these patches. In order to maximize the rate of gain of some currency from these patches, foragers should stay in patches for some optimal time, which may be predicted if the gain function is known (Krebs & McCleery 1984).

In a series of experiments, the behaviour of sheep grazing in a patchy environment was investigated. Individual sheep were introduced to ryegrass paddocks containing transplanted good patches of ryegrass, which were fertilised, darker green and taller than the unfertilised background sward. On different experimental days, the travel time between the preferred patches was varied by either hobbling sheep or transplanting patches at different densities. The mean travel times and mean patch residence times for first visits to patches were calculated for each experiment. These patches of ryegrass were all structural and biochemical replicates, so that the gain function for a first visit to each patch was similar. A total of three sheep were tested. Gain functions for additional replicate patches of ryegrass were determined for individual sheep in indoor trials. The functions which best described intake curves were smooth and decelerating.

Both hobbling and transplanting patches at greater distances from each other resulted in increased travel times between patches. There was a positive relationship between mean travel time and mean patch residence time. However, in most cases there was no significant agreement between the observed and predicted patch residence times for a first visit to a patch. Sheep 007 stayed in patches for longer than predicted for all travel times, while at greater travel times, both of the other sheep tested also tended to stay in patches for longer than predicted by the marginal value model. One explanation for this result is that the energetic cost of travel between patches was greater than that of grazing from (foraging within) a good ryegrass patch. However, when this difference was taken into account, based on energetic values taken from the literature, the agreement between observed and predicted values did not improve significantly.

One obvious limitation of these experiments was that there were relatively few data collected for the three sheep tested. I was unable to determine whether the responses of sheep to manipulation of travel time by hobbling and varying patch density were similar. It would be of interest to carry out more experiments in which a range of travel times for both hobbles and different patch densities are obtained in order to make this comparison. In my calculations I assumed that there was no additional energetic cost on travel imposed by hobbling, but there may well have been some cost, particularly since there were hobble lengths at which sheep refused to move even though movement was possible. An additional drawback of the design of field experiments was that sheep had to pass through a gateway to reach another paddock. This added variation to travel time between good patches, and in future experiments it might be more suitable to work in a larger paddock area without subdividing fences. It would also be useful to determine the effect of various structural sward parameters on the form of the gain functions for sheep grazing on swards of ryegrass.

In summary, the results of the above experiments indicate that sheep respond to patchiness in their grazing environment, and that their foraging behaviour is constrained by travel time between good patches. In addition these results suggest that grazing behaviour of sheep may be explained by intake rate-maximizing rules, although not necessarily by so simple a model as the marginal value theorem. Alternative foraging models predict that under some circumstances, foragers may stay in patches for longer than predicted by the marginal value theorem (Stephens & Krebs 1986). These models take account of the state of the forager's state of hunger and variation in how it may value present and future foraging gains (Stephens & Krebs 1986).

5.3 Further unanswered questions

While the results presented in this thesis have answered some of the questions raised about grazing behaviour and diet selection of domestic vertebrate herbivores, they have raised further questions and identified areas for future investigation, which are outlined below.

(1) The extent to which sward structure and nutritional content of perennial ryegrass interact to influence grazing preferences of sheep is still unclear as is their interaction with other physical sward

parameters such as brightness and toughness of vegetation. Only by further controlled grazing experiments and choice trials can their relative importance be elucidated. Although these factors may often be correlated, the methods described in this study and those used by Kenney & Black (1984) have illustrated some of the ways in which these problems may be surmounted.

(2) The role of learning in diet selection by herbivores is only beginning to be investigated, although it has long since begun to be speculated upon by researchers (Westoby 1974; Zahorik & Houpt 1981). The mechanisms by which sheep may learn to associate cues such as brightness, toughness, and sward height with various physiological consequences remain to be resolved. However, data from colour discrimination experiments suggest that sheep are able to learn associations rapidly (C. V. Ensor & D. R. Bazely unpubl. data).

(3) While my experiments did not control for the sense of smell being used to locate good patches from a distance, it seemed likely that sheep relied mainly upon sight. The role of sight in diet selection in herbivores has been largely ignored, and the results of the experiments in which sward brightness was manipulated taken in conjunction with other recent research (Kendrick & Baldwin 1987; C. V. Ensor & D. R. Bazely unpubl. data) indicate that this particular sense deserves more attention.

(4) Finally, the experimental and theoretical approach to grazing behaviour provided by optimal foraging theory appears to deserve greater attention in future research, particularly the patch-use models. It would of great interest to extend them in order to incorporate nutrient and energetic constraints, and to determine which currencies (nitrogen, dry matter intake etc.) are of importance to herbivores. Also, these models should be extended to take account of social interactions between grazing animals. More recent developments in foraging theory which have moved beyond the simple "classical" foraging models would also be of use in the study of grazing behaviour since they consider problems such as those of a forager which must track a changing environment (Stephens & Krebs 1986). Herbivores as much as other foragers are continually dealing with a fluctuating environment, but apart from Westoby's (1974) and Crawley's (1983) discussion of the role of sampling, this aspect of grazing behaviour has hardly been investigated. Thus, the greatest use of OFT to the study of grazing behaviour is probably that it provides a fresh experimental approach.

Appendix 2.1

Glossary of terms used in studies of grazing and grass growth

Definitions and explanatory notes given below are based on those in Arber (1934), Hodgson (1979), Langer (1979), Hodgson *et al.*. (1986). The reader is referred to these references for more detailed discussion.

Foliar organ	A plant leaf or foliar organ, technically consists of a number of morphological units in addition to the leaf blade. Thus, the term foliar organ is more precise than the term "leaf" which is often incorrectly used to describe only the blade or lamina.
Lamina	A grass tiller is composed of a number of foliar organs, each composed of a lamina and leaf sheath (Figure A 2.1). The lamina is the "leaf blade" of a grass leaf, and at its junction with the sheath is the ligule.
Lamina length	In this thesis the term refers to the length of the longest live lamina on a tiller measured from the junction with the leaf sheath to the tip of the lamina. Measured tillers were selected at random from a core or tray of perennial ryegrass.
Leaf axil	Area subtended by the stem and leaf (Figure A 2.1)
Leaf sheath	Tightly rolled segment of each foliar organ on a tiller (Figure A 2.1). Each leaf sheath and lamina arises from a node at the base of the tiller.
Ligule	Membranous structure at the junction of the lamina and leaf sheath (Figure A 2.1).
Perennial ryegrass	Perennial ryegrass (*Lolium perenne*) is the most commonly grown grass crop in southern England and forms the basis of swards on which most sheep and cattle graze.
Pseudostem	What appears to be the stem of a tiller is in fact a collection of laminae and leaf sheaths tightly rolled or folded on inside the other. The true stem of the tiller which is composed of a series of nodes and highly contracted internodes is extremely short and not visible from the outside (Figure A 2.1).
Pseudostem length	The length from the base of a tiller to the top of the leaf sheath (junction with lamina) of the most recently emerged leaf (Figure A 2.1).
Sward	A population of graminoids and herbaceous plants, characterized by a relatively short habit of growth and relatively continuous ground cover. The term is usually taken to include both above- and below-ground plant parts, but in this thesis refers only to above-ground biomass.
Sward height	Sward heights are taken *in situ* with a sward stick. The base of the stick is placed perpendicular to the soil surface and the height at which the moveable perspex window first makes contact with green leaf when it is gently lowered is taken as one measurement. The perspex window should not be allowed to depress the leaf.
Tiller	The grass plant is composed of a collection of tillers or shoots. A tiller is made up of a number of foliar organs, each composed of a lamina or leaf sheath. Each foliar organ arises from nodes at the base of the tiller (Figure A 2.1). In the axil of each leaf, situated at a node is an axillary bud which under suitable conditions may grow out to become a new tiller.

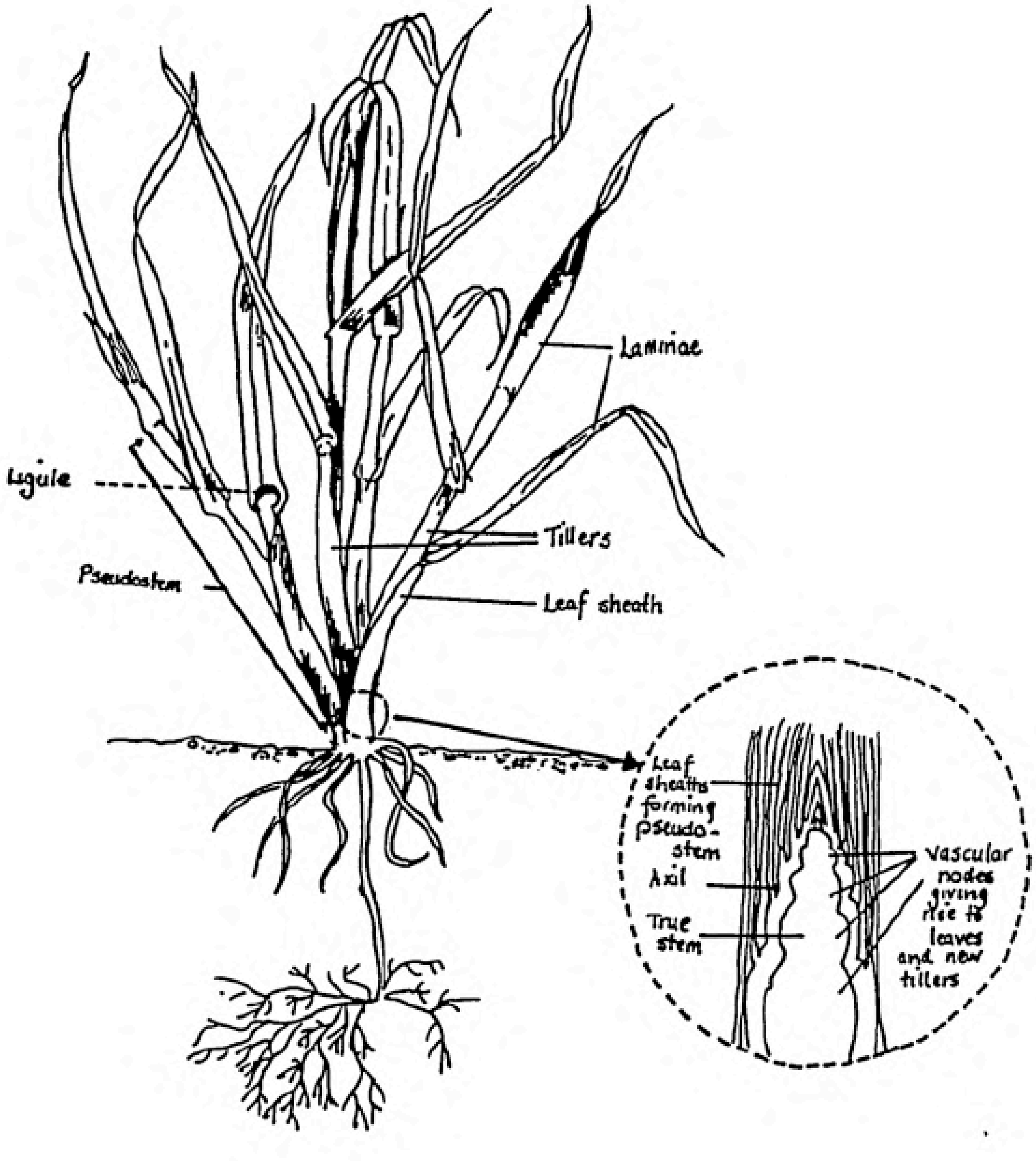


Figure A2.1. Diagram of a grass tiller. The enlarged portion shows the much reduced true stem and the meristem. After Arber (1934) and Langer (1979).

Appendix 2.2

Chemical Analyses

2.2.1 Estimation of modified acid-detergent fibre (MAD Fibre) (MAFF 1981)

"Modified acid-detergent fibre is determined gravimetrically. The sample is boiled with a sulphuric acid solution of cetyltrimethylammonium bromide (CTAB) under controlled conditions. The CTAB dissolves nearly all the nitrogenous constituents and the acid hydrolyzes the starch. The insoluble matter remaining is known as modified acid-detergent fibre." (MAFF 1981, p.82)

Reagents

1. Acetone - technical grade.
2. MS Antifoam A solution. (5M = 10N)
3. Sulphuric acid-CTAB solution: make up 1 litre of 0.5 M sulphuric acid (H_2SO_4) by diluting 100 ml of 5 M H_2SO_4 to 1 litre with distilled and deionized (D & D) water. Dissolve 10 g of CTAB in this solution using a magnetic stirrer.

Procedure

1. Transfer approximately 0.5 g of dried sample, accurately weighed and ground to pass a 1 mm mesh sieve into a 1 l conical flask.
2. Add 50 ml of H_2SO_4-CTAB solution to the flask. Fit a cold-finger condenser, and rapidly bring to a boil on a hot plate.
3. Gently boil for 2.5 hours. While this is happening, weigh warm sinter crucibles (Sintaglass porosity no. 1, 100-120 μm maximum pore diameter) which have been in a drying oven at 95°C.
4. Add 1-2 drops of antifoam to the conical flask containing the sample before filtering. Filter sample and solution hot through the weighed sinter crucible.
5. Wash residue with three portions of approximately 50 ml hot D & D water and then with approximately 50 ml acetone. Repeat if necessary until all colour is washed from residue of sample remaining in the crucible.
6. Dry the crucible in an oven at 95°C overnight.
7. Weigh crucible warm from the oven.
8. Calculate the amount of remaining fibre as a percentage of the original sample weight. This is the MAD fibre content of the sample.
9. Clean sinter crucibles by soaking in a chromic acid bath.

2.2.2 Estimation of water soluble carbohydrate (MAFF 1981)

"Soluble carbohydrates are extracted from herbage with water. The concentration of carbohydrate expressed as glucose in the extract is determined spectrophotometrically as the blue-green complex which is formed when carbohydrates are heated with anthrone in sulphuric acid." (MAFF 1981, p.36)

Reagents

1. Anthrone reagent: Add with stirring, 760 ml of sulphuric acid, approximately 98% m/m H_2SO_4 to 330 ml D &D water. Cool the solution and add 1 g thiourea (NH_2.CS. NH_2. ANALR grade), 1 g anthrone (C_6H_4.CO. C_6H_4.CH_2. ANALR grade) and stir until dissolved. Store in a fridge.
2. Glucose stock standard solution, 0.8 mg/ml of glucose: Dissolve 0.4 g of anhydrous glucose (O.(CH.OH)$_4$.CH.CH_2OH ANALR grade) in D & D water in a 500 ml volumetric flask. Prepare immediately before use.
3. Glucose working standard solutions: Make up solutions containing 0.00, 0.04, 0.08, 0.12, 0.16, and 0.20 mg/ml of glucose in 100 ml volumetric flasks.

Preparation of standard curve

1. Pipette 2 ml of each glucose working solution into a boiling tube. Rapidly add 10 ml of anthrone solution and mix by shaking the test-tube. Loosely cover with a glass stopper (large glass playing marbles were used) and immediately place in a boiling water bath for 20 minutes. Cool for 2-3 minutes and measure the absorbance in a 10 mm cuvette at 625 nm.
2. From these values, a standard curve of optical density (absorbance) against glucose concentration of each 2 ml of standard solution in mg/ml is plotted.
3. Two of these standard solution samples are run with each batch of samples.

Procedure

1. Transfer 0.05-0.09 g of accurately weighed dried and ground plant sample into a 250 ml conical flask. Add 200 ml of D & D water, stopper and shake for 1 hour. Gallenkamp flask shakers were used.
2. Filter through 12.5 cm Whatman no. 1 filter paper, reject the first few ml and retain the filtrate for the determination of soluble carbohydrates, which must be carried out without delay.
3. Pipette 2 ml of extract into a boiling tube (150 mm x 25 mm borosilicate glass). Rapidly add 10 ml of anthrone reagent and mix by shaking the test-tube. Loosely cover with a glass stopper (large glass playing marbles were used) and immediately place in a boiling water bath for 20 minutes. Cool for 2-3 minutes and measure the absorbance in a 10 mm cuvette at 625 nm.
4. Run "blank" samples consisting of shaken and filtered D & D water only through the above boiling procedure and read absorbance on spectrophotometer to check for background traces of water soluble carbohydrate.
5. Calculate carbohydrate content of samples by multiplying glucose concentration of 2 ml of filtrate obtained from standard curve by 200 and dividing by dry weigth of sample originally shaken. This gives the carbohydrate content as mg/g.

2.2.3 Estimation of total nitrogen content (c.f. Allen, Grimshaw & Rowland 1986)

Kjeldahl Digestion

The organic nitrogen content of vegetation is converted to ammonia-nitrogen which can then be readily estimated. The vegetation is digested by sulphuric acid in the presence of salt and a catalyst.

Reagents

1. Selenium catalyst tablets (e.g. Fisons "Kjeldahl catalyst" tablets-selenium)
2. Concentrated sulphuric acid: H_2SO_4 98% ANALR grade.

Procedure

1. Between 40-50 mg of accurately weighed, dried and ground plant sample is placed in a 30 ml, round-bottomed Kjeldahl flask.
2. One selenium tablet and 2.5 ml of conc. H_2SO_4 are added to the sample which is then boiled on a digestion rack for approximately 2 hours or until the acid is completely clear and the sample and tablet are totally digested. The flask may be occasionally turned and gently shaken.
3. After the sample has cooled down, the total volume is made up to 15 ml by the addition of 12.7 ml D & D water.
4. The sample may then be analysed for total nitrogen using an autoanalyser, or if one is unavailable, with a method for the analysis of ammonia-nitrogen, such as that of Solorzano (1969).

Appendix 4.1

Calculations used for determination of change in bite size for sheep grazing on trays of *Lolium perenne*

In calculating bite size in vertebrate herbivores, most researchers have allowed the animal to graze from a sward for a specified period of time, counted the number of bites and calulated the total amount of vegetation removed. They have then divided the total intake by the total number of bites to yield a mean value for bite size. However, this does not take into account the change in bite size that occurs during the observation period (cf. Burlison & Hodgson 1985).

For example, if mean bite size is measured over 1 minute and 2 minute periods for sheep grazing from similar grass patches, the values obtained for these two periods may be very similar if the conventional calculation is used. The following calculation takes account of changes in the rate of cumulative intake during a grazing bout in one patch of grass as mean sward height declines, which may result in rapid changes in bite size. Cumulative intake and number of bites taken during the first minute are removed from the two minute grazing period, and mean bite size is calculated from the remaining biomass and number of bites taken in the remaining minute.

$X_{t_{ij}}$ - dry matter intake at time t_i

$Y_{t_{ij}}$ - number of bites observed in time period t_i

$Z_{t_{ij}}$ - bite size at time t_i

i = time period 1, 2, ...5

1 represents 15 seconds, 2 represents 30 seconds etc.

j = replicate 1, 2, 3 at time t_i

For t_1, which was 15 seconds for all sheep except for 267, when it was 30 seconds, the mean bite size was

$$\overline{Z}_{t_1} = \frac{\sum_{j=1}^{3} Z_{t_{1j}}}{3}$$

where

$$Z_{t_{1j}} = \frac{X_{t_{1j}}}{Y_{t_{1j}}}$$

For calculation of the subsequent changes in mean bite size from t_1 to t_2, t_2 to t_3 etc., the following equation was used:

For $i = 2$

$$Z_{t_{2j}} = \frac{X_{t_{2j}} - \overline{X}_{t_1}}{Y_{t_{2j}} - \overline{Y}_{t_1}}$$

The mean dry matter intake at t_1 was used, rather than individual values, X_{t1j}, because different replicate trays were used to measure intake at t_2 and t_1. Therefore, replicate, $j = 1$ at t_1 was not directly related to $j = 1$ at t_2 in any way.

thus, the mean bite size at the end of time period 2 was

$$\overline{Z}_{t_2} = \frac{\sum_{j=1}^{3} Z_{t_{2j}}}{3}$$

and generally, for $i > 1$

$$Z_{t_{ij}} = \frac{X_{t_{ij}} - \overline{X}_{t_{i-1}}}{Y_{t_{ij}} - \overline{Y}_{t_{i-1}}}$$

$$\overline{Z}_{t_i} = \frac{\sum_{j=1}^{3} Z_{t_{ij}}}{3}$$

Appendix 4.2

Relationships between patch residence times and travel times

Correlation coefficients for patch residence time (seconds) recorded at time $t+1$ regressed on patch residence time at time t. None of the correlation coefficients were significant.

Sheep	Experiment date	Correlation coefficient	df	Sheep	Experiment date	Correlation coefficient	df
007	9 August	0.107	24	25	1 September	0.501	6
007	11 August	0.213	27	25	3 September	0.025	20
007	13 August	0.288	4	25	6 September	0.465	7
007	15 August	0.041	8	25	8 October	0.052	27
007	17 August	0.002	25	211	9 October	0.169	4
007	19 August	0.352	5	211	10 October	0.020	27
007	21 August	0.309	27	211	12 October	0.016	18
007	27 August	0.04	22	211	14 October	0.694	6

Correlation coefficients for individual patch residence times (seconds) regressed upon the preceeding travel times (seconds). None were significant.

Sheep	Experiment date	Correlation coefficient	df	Sheep	Experiment date	Correlation coefficient	df
007	9 August	0.071	24	25	1 September	0.177	6
007	11 August	0.264	27	25	3 September	0.068	22
007	13 August	0.006	4	25	6 September	0.370	7
007	15 August	0.084	8	25	8 October	0.099	24
007	17 August	0.108	25	211	9 October	0.068	4
007	19 August	0.143	5	211	10 October	0.007	25
007	21 August	0.288	27	211	12 October	0.335	15
007	27 August	0.205	22	211	14 October	0.254	6

REFERENCES

Abisgold, J. D. & Simpson, S. J. 1987. The physiology of compensation by locusts for changes in dietary protein. Journal of Experimental Biology 129: 329-346.

Abisgold, J. D. & Simpson, S. J. 1988. The effect of dietary protein levels and haemolymph composition on the sensitivity of the maxillary palp chemoreceptors of locusts. Journal of Experimental Biology In press.

Alder, F. E. & Minson, D. J. 1963. The herbage intake of cattle grazing lucerne and cocksfoot pastures. Journal of Agricultural Science 60: 359-369.

Allden, W. G. 1968. Under-nutrition of the merino sheep and its sequelae. 4. Herbage consumption and utilization of feed for wool production following growth restrictions imposed at two stages of early post-natal life in a mediterranean environment. Australian Journal of Agricultural Research 19: 997-1007.

Allden, W. G. 1981. Energy and protein supplements for grazing livestock. In Morley, F. W. H. (ed.). Grazing Animals: World Animal Science. B. Disciplinary Approach (1). pp. 289-307. Elsevier Scientific Publishing Company, Amsterdam.

Allden, W. G. & Whittaker, I. A. 1970. The determinants of herbage intake by grazing sheep: the inter-relationship of factors influencing herbage intake and availability. Australian Journal of Agricultural Research 21: 755-766.

Allen, S. E., Grimshaw, H. M. & Rowland, A. P. 1986. Chemical Analysis. In Moore, P. D. & Chapman, S. B. (eds.). Methods in Plant Ecology, 2nd Ed. pp. 285-344. Blackwell Scientific Publications, Oxford.

Appleby, M. C. 1980. Social rank and food access in red deer stags. Behaviour 74: 294-309.

Arnold, G. W. 1960a. Selective grazing by sheep of two forage species at different stages of growth. Australian Journal of Agricultural Research 11: 1026-1033.

Arnold, G. W. 1960b. The effect of the quantity and quality of pasture available to sheep on their grazing behaviour. Australian Journal of Agricultural Research 11: 1034-1043.

Arnold, G. W. 1962. Effects of pasture maturity on the diet of sheep. Australian Journal of Agricultural Research 13: 701-706.

Arnold, G. W. 1963. The diet of the grazing sheep. Ph.D. Thesis. London University, U. K.

Arnold, G. W. 1964. Plant associations affecting grazing animals. In Crisp, D. J. (ed.). Grazing in Terrestrial and Marine Environments. pp. 133-154. British Ecological Society Symposium no. 4. Blackwell Scientific Publications, Oxford.

Arnold, G. W. 1966a. The special senses in grazing animals. I. Sight and dietary habits in sheep. Australian Journal of Agricultural Research 17: 521-529.

Arnold, G. W. 1966b. The special senses in grazing animals. II. Smell, taste and touch and dietary habits in sheep. Australian Journal of Agricultural Research 17: 531-542.

Arnold, G. W., Ball, J., McManus, W. R. & Bush, I. G. 1966. Studies on the diet of the grazing animal. I. Seasonal changes in the diet of sheep grazing on pastures of different availability and composition. Australian Journal of Agricultural Research 17: 543-556.

Arnold, G. W. & Dudzinski, M. L. 1978. Ethology of free-ranging domestic animals. Elsevier Scientific

Publishing Co., Amsterdam.

Arnold, G. W., de Boer, E. S. & Boundy, C. A. P. 1980. The influence of odour and taste on the food preferences and food intake of sheep. Australian Journal of Agricultural Research 31: 571-587.

Backhaus, D. von. 1959. Visual acuity in Ungulates. Zeitschrift fur Tierpsychologie 16: 445-467.

Bakker, J. P., de Leeuw, J. & van Wieren, S. E. 1983. Micro-patterns in grassland vegetation created and sustained by sheep-grazing. Vegetatio 55: 153-161.

Barber, W. P, Adamson, A. H. & Altman, J. F. B. 1984. New methods of forage evaluation. In Haresign, W. & Cole, D. J. A. (eds.). Recent Advances in Animal Nutrition-1984. pp. 161-176. Butterworths, London.

Barthram, G. T. 1981. Sward structure and the depth of the grazed horizon. Grass and Forage Science 36: 130-131.

Begon, M., Harper, J. L. & Townsend, C. R. 1986. Ecology: Individuals, Populations and Communities. Blackwell Scientific Publications, Oxford.

Belovsky, G. E. 1978. Diet Optimization in a Generalist Herbivore: The Moose. Theoretical Population Biology 14: 105-134.

Belovsky, G. E. 1981. Food Plant Selection by a Generalist Herbivore: The Moose. Ecology 62: 1020-1030.

Belovsky, G. E. 1984a. Snowshoe Hare Optimal Foraging and its Implications for Population Dynamics. Theoretical Population Biology 25: 235-264.

Belovsky, G. E. 1984b. Herbivore Optimal Foraging: a Test of Three Models. American Naturalist 124: 97-115.

Binnie, R. C., Harrington, F. J. & Murdoch, J. C. 1974. The effect of cutting height and nitrogen level on the yield, *in vitro* digestibility and chemical composition of Italian ryegrass swards. Journal of the British Grassland Society 29: 57-62.

Black, J. L. & Kenney, P. A. 1984. Factors affecting diet selection by sheep. II. Height and density of pasture. Australian Journal of Agricultural Research 35: 565-578.

Bland, B. F. & Dent, J. W. 1964. Animal preference in relation to the chemical composition and digestibility of varieties of cocksfoot. Journal of the British Grassland Society 19: 306-315.

Blaser, R. E., Hammes, R. C., Bryant, H. T., Hardison, W. A., Fontenot, J. P. & Engel, R. W. 1960. The effect of selective grazing on animal output. Proceedings of 8th International Grasslands Congress. pp. 601-606.

Blaxter, K. L. 1967. The Energy Metabolism of Ruminants. Hutchinson Scientific and Technical, London.

Broom, D. M. 1981. Biology of Behaviour: Mechanisms, functions and applications. Cambridge University Press, Cambridge.

Bryant, J. P. & Kuropat, P. J. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. Annual Review of Ecology and Systematics 11: 261-285.

Buckner, R. C., Todd, J. R., Burrus, P. B. & Barnes, R. F. 1967. Chemical composition, palatability and digestibility of Ryegrass-Tall Fescue Hybrids 'Kenwell' and 'Kentucky 31' Tall Fescue varieties. Agronomy Journal 59: 345-349.

Burlison, A. J. & Hodgson, J. 1985. The influence of sward structure on the mechanics of the grazing process in sheep. Animal Production 40: 530-531.

Burton, G. W., Knox, F. E. & Beardsley, D. W. 1964. Effect of age on the chemical composition, palatability and digestibility of grass leaves. Agronomy Journal 56: 160-161.

Cahn, M. A. & Harper, J. L. 1976. The biology of the leaf mark polymorphism in *Trifolium repens* L. II. Evidence for the selection of leaf marks in rumen fistulated sheep. Heredity 37: 327-333.

Cargill, S. M. & Jefferies, R. L. 1984. The effects of grazing by Lesser Snow Geese on the vegetation of a sub-arctic salt marsh. Journal of Applied Ecology 21: 669-686.

Chapple, R. S., Wodzicka-Tomaszewska, M. & Lynch, J. J. 1987a. The learning behaviour of sheep when introduced to wheat. I. Wheat acceptance by sheep and the effect of trough familiarity. Applied Animal Behaviour Science 18: 157-162.

Chapple, R. S., Wodzicka-Tomaszewska, M. & Lynch, J. J. 1987b. The learning behaviour of sheep when introduced to wheat. II. Social transmission of wheat feeding and the role of the senses. Applied Animal Behaviour Science 18: 163-172.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. Theoretical Population Biology 9: 129-136.

Clutton-Brock, T. H. (ed.). 1977. Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. Academic Press, London.

Corrall, A. J., Lavender, R. H. & Terry, C. P. 1979. Grass species and varieties: seasonal patterns of production and relationships between yield, quality and date of first harvest. Technical Report no. 26. Grassland Research Institute, Hurley, U. K.

Cowie, R. J. 1977. Optimal foraging in great tits *Parus major*. Nature 268: 137-139.

Cowlishaw, S. J. & Alder, F. E. 1960. The grazing preferences of cattle and sheep. Journal of Agricultural Science 54: 257-265.

Crawley, M. J. 1983. Herbivory: the dynamics of animal-plant interactions. Blackwell Scientific Publications, Oxford.

Crofton, H. D. 1952. The ecology of immature phases of trichstrongyle nematodes. IV. Larval populations on lowland pastures. Parasitology 42: 77-84.

Cropper, M., Lloyd, M. D. & Emmans, G. C. 1985. An investigation into the relationship between nutrient requirements and diet selection in growing lambs. Animal Production 40: 562.

Denton, D. A. & Sabine, J. R. 1963. The behaviour of Na deficient sheep. Behaviour 20: 364-376.

Eadie, J. 1970. Sheep production and pastoral resources. In Watson, A. (ed.). Animal Populations in Relation to Their Food Resources. pp. 7-24. British Ecological Society Symposium no. 10. Blackwell Scientific Publications, Oxford.

Evans, P. S. 1964. A study of leaf strength in four ryegrass varieties. New Zealand Journal of Agricultural Research 7: 508-513.

Evans, P. S. 1967a. Leaf strength studies of pasture grasses. I. Apparatus, techniques and some factors affecting leaf strength. Journal of Agricultural Science 69: 171-174.

Evans, P. S. 1967b. Leaf strength studies of pasture grasses. II. Strength, cellulose content and sclerenchyma tissue proportions of eight grasses grown as single plants. Journal of Agricultural Science 69: 175-181.

Fontenot, J. B. & Blaser, R. E. 1965. Symposium on factors influencing voluntary intake of herbage by ruminants: selection and intake of grazing animals. Journal of Animal Science 24: 1202-1208.

Freer, M. 1981. The control of food intake by grazing animals. In Morley, F. W. H. (ed.). Grazing Animals: World Animal Science. B. Disciplinary Approach (1). pp. 105-124. Elsevier Scientific Publishing Company, Amsterdam.

Glander, K. E. 1981. Feeding Patterns in Mantled Howler Monkeys. In Kamil, A. C. & Sargent, T. D. (eds.). Foraging Behaviour: Ecological, Ethological and Psychological Approaches. pp. 231-258. Garland STPM Press, New York.

Grant. S. A., Suckling, D. E., Smith, H. K., Torvell, L., Forbes, T. D.A. & Hodgson, J. 1985. Comparative studies of diet selection by sheep and cattle: the hill grasslands. Journal of Ecology 73: 987-1004.

Gray, R. D. 1987. Faith and Foraging: A Critique of the Paradigm Argument from Design. In Kamil, A. C., Krebs, J. R. & Pulliam, H. R. (eds.). Foraging Behavior. pp. 69-142. Plenum Press, New York.

Greenwood, J. J. D. & Elton, R. A. 1979. Analysing experiments on frequency-dependant selection by predators. Journal of Animal Ecology 48: 721-737.

Hacker, J. B. 1982. Selecting and breeding better quality grasses. In Hacker, J. B. (ed.). Nutritional Limits to Animal Production From Pastures. pp. 305-326. Proceedings of an International Symposium, St. Lucia, Queensland, Australia. Commonwealth Agricultural Bureaux, Farnham Royal, U. K.

Hairston, N. G., Smith, F. E. & Slobodkin, L. B. 1960. Community structure, population control and competition. American Naturalist 94: 421-425.

Hamilton, B. A., Hutchison, K. J., Annis, P. C. & Donnelly, J. B. 1973. Relationships between the diet selected by grazing sheep and the herbage on offer. Australian Journal of Agricultural Research 24: 271-277.

Hardison, W. A., Reid, J. T., Martin, C. M. & Woolfolk, P. G. 1954. Degree of herbage selection by grazing cattle. Journal of Dairy Science 37: 89-102.

Harper, J. L. 1977. Population Biology of Plants. Academic Press, London.

Harwood, J. 1975. The grazing strategies of blue geese *Anser caurulescens*. Ph.D. Thesis. University of Western Ontario, Canada.

Hodgson, J. 1968. The relationship between the digestibility of a sward and the herbage consumption of grazing calves. Journal of Agricultural Science 70: 47-51.

Hodgson , J. 1979. Nomenclature and definitions in grazing studies. Grass and Forage Science 34: 11-18.

Hodgson, J. 1982. Influence of sward characteristics on diet selection and herbage intake by the grazing animal. In Hacker, J. B. (ed.). Nutritional Limits to Animal Production From Pastures. pp. 153-166. Proceedings of an International Symposium, St. Lucia, Queensland, Australia. Commonwealth Agricultural Bureaux, Farnham Royal, U. K.

Hodgson, J. 1984. Sward conditions, herbage allowance and animal production: an evaluation of research results. Proceedings of New Zealand Society of Animal Production 44: 99-104.

Hodgson, J., Mackie, C. K. & Parker, J. W. G. 1986. Sward surface heights for efficient grazing. Grass Farmer 24: 5-10.

Iason, G. R., Duck, C. D. & Clutton-Brock, T. H. 1986. Grazing and reproductive success of red deer: the effect of local enrichment by gull colonies. Journal of Animal Ecology 55: 507-515.

Illius, A. W. & Gordon, I. J. 1987. The allometry of food intake in grazing ruminants. Journal of Animal Ecology 56: 989-999.

Jacobs, G. H. 1981. Comparative Color Vision. Academic Press, New York.

Kacelnik, A. 1984. Central place foraging in starlings (*Sturnus vulagaris*). 1. Patch residence time. Journal of Animal Ecology 52: 283-300.

Kacelnik, A. & Cuthill, I. C. 1987. Starlings and Optimal Foraging Theory: Modelling in a Fractal World. In Kamil, A. C., Krebs, J. R. & Pulliam, H. R. (eds.). Foraging Behavior. pp. 303-334. Plenum Press, New York.

Kacelnik, A. & Houston, A. I. 1984. Some effects of energy costs on foraging strategies. Animal Behaviour 32: 609-614.

Kacelnik, A., Houston, A. I. & Krebs, J. R. 1981. Optimal foraging and territorial defence in the great tit *Parus major*. Behavioural Ecology and Sociobiology 8: 35-40.

Kendrick, K. M. & Baldwin, B. A. 1987. Cells in temporal cortex of conscious sheep can respond preferentially to the sight of faces. Science 236: 448-450.

Kenney, P. A. & Black, J. L. 1984. Factors affecting diet selection by sheep. I. Potential intake rate and acceptability of feed. Australian Journal of Agricultural Research 35: 551-563.

Krebs, J. R. & McCleery, R. H. 1984. Optimization in Behavioural Ecology. In Krebs, J. R. & Davies, N. B. (eds.). Behavioural Ecology: An Evolutionary Approach, 2nd Ed. pp. 91-121. Blackwell Scientific Publications, Oxford.

Krebs, J. R., Houston, A. I. & Charnov, E. L. 1981. Some Recent Developments in Optimal Foraging. In Kamil, A. C. & Sargent, T. D. (eds.). Foraging Behaviour: Ecological, Ethological and Psychological Approaches. pp. 3-18. Garland STPM Press, New York.

Krebs, J. R., Stephens, D. W. & Sutherland, W. J. 1983. Perspectives in optimal foraging. In Brush, A. H. & Clark, G. A. (eds.). Perspectives in Ornithology. pp. 165-216. Cambridge University Press, New York.

Laidlaw, A. S. 1983. Grazing by sheep and the distribution of species through the canopy of a red clover-perennial ryegrass sward. Grass and Forage Science 38: 317-321.

Lambert, J. 1982. Selectivity of grazing in sheep. M.Sc. Thesis. University College of North Wales, Bangor, U. K.

Lawrence, A. B. & Wood-Gush, D. G. M. 1988. Influence of social behaviour on utilization of supplemental feedblocks by Scottish hill sheep. Animal Production 46: 203-212.

Marten, G. C. & Donker, J.D. 1964. Selective grazing induced by animal excreta. II. Investigation of a causal theory. Journal of Dairy Science 47: 871-874.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11: 119-161.

McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. American Naturalist 124: 863-886.

McNaughton, S. J. 1986. Grazing lawns: on domesticated and wild grazers. American Naturalist 128: 937-939.

Miller, G. D. 1986. Feeding ecology of desert bighorn sheep (*Ovis canadensis mexicana*) in western Arizona. Ph.D. Dissertation. New Mexico University, Albuquerque, New Mexico.

Milton, W. E. J. 1933. The palatability of the self-establishing species contributing to different types of grassland. Empire Journal of Experimental Agriculture 1: 347-359.

Ministry of Agriculture, Fisheries and Food. 1981. The Analysis of Agricultural Materials. 2nd Ed. MAFF Technical Bulletin RB 427. HMSO, London.

Minson, D. J. 1976. Nutritional significance of protein in temperate and tropical pastures. In Sutherland, T. M., McWilliam, J. R. & Leng, R. A. (eds.). Reviews in Rural Science II. pp. 27-30. University of New England Publishing Unit, Armidale, New England.

Myers, J. H. 1985. Effect of physiological condition of the host plant on the ovipositional choice of the cabbage white butterfly, *Pieris rapae*. Journal of Animal Ecology 54: 193-204.

Norton, B. W. 1982. Differences between species in forage quality. In Hacker, J. B. (ed.). Nutritional Limits to Animal Production From Pastures. pp. 89-110. Proceedings of an International Symposium, St. Lucia, Queensland, Australia. Commonwealth Agricultural Bureaux, Farnham Royal, U. K.

Olsen, J. D. & Ralphs, M. H. 1986. Feed aversion induced by intra-ruminal infusion with larkspur extract in cattle. American Journal of Veterinary Research 47: 1829-1833.

Ørskov, E. R. 1982. Protein Nutrition in Ruminants. Academic Press, London.

Osuji, P. O. 1974. The physiology of eating and the energy expenditure of the ruminant at pasture. Journal of Range Management 27: 437-443.

Overmann, S. R. 1976. Dietary self-selection by animals. Psychological Bulletin 2: 218-235.

Owen, M., Nugent, M. & Davies, N. 1977. Discrimination between grass species and nitrogen-fertilized vegetation by young Barnacle Geese. Wildfowl 28: 21-26.

Owen-Smith, N. & Novellie, P. 1982. What should a clever ungulate eat? American Naturalist 119: 151-178.

Parker, M. A. 1984. Local food depletion and the foraging behaviour of a specialist grasshopper, *Hesperotettix viridis*. Ecology 65: 824-835.

Penning, P. D. 1986. Some effects of sward conditions on grazing behaviour and intake by sheep. In Gudmundsson, O. (ed.). Grazing Research at Northern Latitudes. pp. 219-226. Plenum Publishing Corporation, New York.

Penning, P. D., Steel, G. L. & Johnson, R. H. 1984. Further development and use of an automatic recording system in sheep grazing studies. Grass & Forage Science 39: 345-351.

Pietrewicz, A. T. & Kamil, A. C. 1981. Search Images and the Detection of Cryptic Prey: An Operant Approach. In Kamil, A. C. & Sargent, T. D. (eds.). Foraging Behaviour: Ecological, Ethological and Psychological Approaches. pp. 311-331. Garland STPM Press, New York.

Plice, M. J. 1951. Sugar versus the intuitive choice of food by livestock. Journal of Range Management

5: 69-74.

Price, M. R. S. 1978. The nutritional ecology of Coke's hartebeest (*Alcelaphus buselaphus cokei*) in Kenya. Journal of Applied Ecology 15: 33-49

Provenza, F. D. & Balph, D. F. 1987. Diet Learning by Domestic Ruminants: Theory, Evidence and Practical Implications. Applied Animal Behaviour Science 18: 211-232.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. Annual Review of Ecology and Systematics 15: 523-575.

Rae, A. L., Brougham, R. W. & Barton, R. A. 1964. A note on liveweight gains of sheep grazing on different ryegrass pastures. New Zealand Journal of Agricultural Research 7: 491-495.

Reid, R. L., Odhuba, E. K. & Jung, G. A. 1967. Evaluation of Tall Fescue pasture under different fertilisation treatments. Agronomy Journal 59: 265-271.

Richter, C. P. 1943. Total self-regulatory functions in animals and human beings. Harvey Lectures 38: 63-103

Robbins, C. T. 1983. Wildlife Feeding and Nutrition. Academic Press, New York.

Rohlf, F. J. & Sokal, R. R. 1981. Statistical Tables, 2nd Ed. W. H. Freeman & Co., New York.

Rutter, S. M., Jackson, D. A., Johnson, C. L. & Forbes, J. M. 1987. Automatically recorded competitive feeding behaviour as a measure of social dominance in dairy cows. Applied Animal Behaviour Science 17: 41-50.

Sadul, H. A. 1987. The effects of Lesser Snow Goose grazing on sub-arctic coastal plant populations. M.Sc. Thesis, University of Toronto.

Shettleworth, S. J. 1984. Learning and Behavioural Ecology. In Krebs, J. R. & Davies, N. B. (eds.). Behavioural Ecology: An Evolutionary Approach, 2nd Ed. pp.170-194. Blackwell Scientific Publications, Oxford.

Simpson, J. R. & Stobbs, T. H. 1981. Nitrogen supply and animal production from pastures. In Morley, F. W. H. (ed.). Grazing Animals: World Animal Science. B. Disciplinary Approach (1). pp. 261-287. Elsevier Scientific Publishing Company, Amsterdam.

Sinclair, A. R. E. 1975. The resource limitations of trophic levels in tropical grassland ecosystems. Journal of Animal Ecology 44: 497-520.

Slater, P. J. B. & Lester, N. P. 1982. Minimizing errors in splitting behaviour into bouts. Behaviour 79: 153-161.

Snodderly, D. M. 1979. Visual discriminations encountered in food foraging by a neotropical primate: Implications for the evolution of color vision. In Burtt, E. H. (ed.). The Behavioral Significance of Color. pp. 237-279. Garland STPM Press, New York.

Sokal, R. R. & Rohlf, F. J. 1981. Biometry. 2nd Ed. W. H. Freeman & Co., New York.

Solorzano, L. 1969. Determination of ammonia in natural waters by the phenol-hypochlorite method. Limnology and Oceanography 14: 799-801.

Stephens, D. W. & Krebs, J. R. 1986. Foraging Theory. Princeton University Press, Princeton, New Jersey.

Thorhallsdottir, A. G., Provenza, F. D. & Balph, D. F. 1987. Food aversion learning in lambs with or without a mother: discrimination, novelty and persistence. Applied Animal Behaviour Science 18: 327-340.

Thouless, C. R. 1986. Feeding competition in red deer hinds. Ph.D. Thesis. University of Cambridge, Cambridge.

Tribe, D. E. 1949. The importance of the sense of smell to the grazing sheep. Journal of Agricultural Science 39: 309-313.

Tribe, D.E. 1950a. The behaviour of the grazing animal: a critical review of present knowledge. Journal of the British Grassland Society 5: 209-224.

Tribe, D. E. 1950b. The composition of a sheep's natural diet. Journal of the British Grassland Society 5: 81-91.

Tribe, D. E. & Gordon, J. G. 1949. The importance of colour vision to the grazing sheep. Journal of Agricultural Science 39: 313-314.

Tuenissen, W., Spaans, B. & Drent, R. 1985. Breeding success in Brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. Ardea 73: 109-119.

Van Soest, P. J. 1982. Nutritional Ecology of the Ruminant. O & B Books, Inc., Corvallis, Oregon.

Wakefield, G. L. 1970. Practical Sensitometry. Fountain Ltd., London.

Warmke, H. E., Freyre, R. H. & Morris, M. P. 1952. Studies on the palatability of some tropical legumes. Agronomy Journal 44: 517-520.

Weir, W. C. & Torell, D. T. 1959. Selective grazing by sheep as shown by a comparison of the chemical composition of range and pasture forage obtained by hand clipping and that collected by osophageal-fistulated sheep. Journal of Animal Science 18: 641-649.

Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. American Naturalist 108: 290-304.

Westoby, M. 1978. What are the biological bases of varied diets? American Naturalist 112: 627-631.

Westoby, M. 1985. Does grazing improve the food resources for grazers? American Naturalist 128: 870-871.

Westoby, M. 1986. Mechanisms influencing grazing success for livestock and wild herbivores. American Naturalist 128: 940-941.

Whitteridge, D. 1978. The development of the visual system in the sheep. Archives Italiennes de Biologie 116: 406-408.

Wilson, J. R. & Minson, D. J. 1980. Prospects for improving the digestibility and intake of tropical grasses. Tropical Grasslands 14: 253-259.

Zahorik, D. M. & Houpt, K. A. 1981. Species Differences in Feeding Strategies, Food Hazards and the Ability to Learn Food Aversion. In Kamil, A. C. & Sargent, T. D. (eds.). Foraging Behaviour: Ecological, Ethological and Psychological Approaches. pp. 289-310. Garland STPM Press, New York.