Diet preference for grass and legumes in
free-ranging domestic sheep and cattle:
Current theory and future application

Steven Mark Rutter*

Institute of Grassland and Environmental Research, North Wyke, Okehampton,
Devon EX20 2SB, United Kingdom

Available online 3 February 2006

Abstract

This paper reviews the current theory and potential practical applications of research on the diet preference for grass and legumes in grazing domestic sheep and cattle. Although much of this work has focussed on grass and clover as a model system, it has wider theoretical implications and potential for practical exploitation. Research in this field is of particular relevance with the recent increased interest in maintaining and enhancing biodiversity, both in agricultural systems and semi-natural habitats. One of the most consistent findings of previous research is that sheep and cattle both eat mixed diets, showing a partial preference of approximately 70% for clover. There is a diurnal pattern to preference, with a stronger preference for clover in the morning, with the proportion of grass in the diet increasing towards the evening. Research has also shown that sheep and dairy cattle achieve higher intakes from grass and clover when these are offered as separate monocultures compared with animals grazing a traditional mixed sward. The initial findings were from studies where the animals had free choice, but similar results have been achieved in dairy cows being allocated to clover between morning and afternoon milking and grass for the remainder of the day. The intake benefits, which have been attributed to a lower selection cost, have the potential to be exploited on-farm to increase intake and production. Our increasing understanding of the factors influencing diet selection raises the possibility of developing grazing management practices to maintain and possibly enhance biodiversity. Various theories have been proposed to account for the fact that ruminants eat mixed
diets. Although some, such as spatial memory and visual discrimination have been discounted, others, such as perceived predation risk and balancing nutrient intake, appear to be more valid. However, further research is still needed to explore and validate hypotheses related to these theories. © 2005 Elsevier B.V. All rights reserved.

Keywords: Diet preference; Selection; Mixed diets; Grass; Clover; Ruminants

1. Introduction

Free-ranging domestic herbivores generally self-select what to eat from the choice available to them (Dumont and Gordon, 2003). Intensification of Western agriculture following the Second World War generally resulted in this choice being restricted to selecting plant components from a ryegrass monoculture, although this trend now appears to be declining. Increased use of legumes, principally to provide nitrogen, in pastures in recent years gives grazing livestock the opportunity to select from at least two different plant species i.e. either a grass or a legume. Further, the desire to maintain and enhance biodiversity has seen a greater interest in grazing to promote biodiversity in pastures (Rook et al., 2004). These developments have increased the need for research to understand the complex interactions between plants and the animals that graze them, with diet preference and selection being important components within these interactions. To date, much of the research into diet preference and selection in grazing domestic ruminants has focussed on domestic sheep and cattle as animal subjects and used perennial ryegrass (Lolium perenne L., hereafter referred to as grass) and white clover (Trifolium repens L., hereafter referred to as clover) as model plant species. This paper reviews this research, summarises the major findings and discusses the various theories proposed to account for the results. Whilst much of this research has been carried out by the author’s own group, this review endeavours to cover all of the existing work on diet selection for grass and clover in grazing sheep and cattle. Although the range of animal and plant species studied have to date been limited, the theoretical aspects have much wider applicability. The research has also resulted in the development of novel grazing strategies that can enhance production from grazing stock, and these are also discussed.

2. General methods

2.1. Preference versus selection

It is important to distinguish between what the animals ‘want’ to eat and what they actually eat because of some external constraint (Parsons et al., 1994). The first of these can be defined as ‘preference’ (Parsons et al., 1994, “what the animals select given the minimum physical constraints”), whereas the second can be defined as ‘selection’ (Hodgson, 1979, “preference modified by environmental circumstances”). For example, animals offered a sward containing grass and clover in an intimate mixture have to search through the mixture to find their preferred herbage. This requirement to search imposes a
constraint on the animal’s ability to eat what it wants, so is an example of selection. In order to measure preference, we need to remove the constraint of the requirement to search through the mixture. This is typically achieved in grazing preference studies by giving the animals a free choice of grazing from adjacent, separate monocultures of grass and clover. That is, part of the treatment paddock is sown as a contiguous monoculture of clover, with the remaining part sown as a contiguous monoculture of grass, and the animals are allowed to graze at will across the two monocultures.

2.2. Indifference versus active selection

Another important part of any study aiming to determine diet preference is an experimental design capable of distinguishing between indifference and active selection (Parsons et al., 1994). For example, suppose that animals grazing a paddock consisting of an area of grass alongside an equal sized area of clover (i.e. 50% grass and 50% clover by ground area) selected a diet consisting of 50% grass and 50% clover. One would not be able to tell if this was an active selection for a diet consisting of 50% grass and 50% clover or whether the animals were just grazing at random (i.e. indifference), and ate 50:50 because that is what they encountered. This problem can be overcome by using at least two treatments offering differing proportions of grass and clover (e.g. 20:80 and 80:20). In this second example, if the animals ate 20:80 and 80:20 in the two treatments, respectively (i.e. the same proportion as was offered in each treatment) it would indicate that they were grazing at random, whereas if their diet choice was similar in both treatments (e.g. 50:50) it would indicate active selection.

2.3. Measuring preference

Although automatic grazing behaviour recording systems are available (e.g. Rutter et al., 1997a), these are unable to determine the plant species being eaten, so cannot record preference. Given that preference studies use spatially separated grass and clover monocultures, it would be possible to automatically record grazing on grass and clover separately if the location of the animal’s grazing was known. Whilst it is possible to track and record the grazing location of domestic animals using GPS (e.g. Rutter et al., 1997b), current GPS-based animal tracking systems lack the precision to determine with any accuracy whether the animal is on the grass or clover part of the paddock. Consequently, the commonest approach to recording preference is through manual scan sampling. The sampling interval should be no more than 5 min (Rook and Huckle, 1997), with the animals behaviour (typically ‘eating’, ‘ruminating’ or ‘idling’) and its location (grass or clover) being recorded at each interval. The observer may have difficulty distinguishing the plant species being consumed when the animals are grazing on the boundary between the two monocultures. There are two approaches typically adopted to deal with this. Firstly, grazing on the boundary can be recorded separately, and assumed to be half grass and half clover in the analysis. Alternatively, the herbage along the boundary can be removed to ground level in a strip, typically approximately 1 m wide, to allow the observer to clearly see which herbage the animal is consuming.

Ideally, the animals would be observed continuously for 24 h a day, using night-vision apparatus to record grazing at night. However, apart from being impractical, it is often
unnecessary to record grazing at night as sheep (Champion et al., 1994) and cattle (Gibb et al., 1998) usually avoid grazing during the hours of darkness, at least in temperate countries. Consequently, preference observations are typically carried out only during the hours of daylight. Although Champion et al. (1994) showed that a 24 h recording could be taken as representative of grazing behaviour over a longer period (7 days in their study), previous experience has been shown to have an effect on diet preference (Parsons et al., 1994). This needs to be taken into account in preference studies, as sheep prefer herbage that was previously lacking in the diet (Parsons et al., 1994). Although this effect is quite short-lived, it is common practice to keep the animals on a ‘background’ paddock that offers the animals the choice of grazing from spatially separated grass and clover monocultures (i.e. the same as in the treatment) for several days prior to the start of the experimental measurements. Potential side biases and preferences are usually dealt with by ensuring that the different replicate paddocks are oriented in different directions relative to, for example, north and south, slope, etc., and water troughs are typically located on the boundary between the two herbage to prevent any bias. The animals are usually introduced onto the paddock (both at the start of the study and when subsequently returning, for example, after milking) on the boundary.

Although the ratio of the time grazing grass and clover can be used to determine preference, various studies have shown that both sheep (Penning et al., 1991) and cattle (Rutter et al., 2004a) often eat clover more quickly than grass. Consequently, grazing time alone is likely to under-estimate the daily intake (in terms of kg DM day\(^{-1}\)) of clover and over-estimate the intake of grass, and so under-estimate preference for clover. Given that daily intake is of more importance than grazing time, both to the animal itself and for production from a domesticated animal, preference should ideally be based on the relative intakes of the two herbage. One way to achieve this is to make short-term measurements of intake, separately for grass and clover, using the technique developed by Penning and Hooper (1985). Given that intake rates can change over the course of the day (Gibb et al., 1998), these intake measurements should be made, at least, at two different times of day. For a given herbage (i.e. either grass or clover), the daily intake of that herbage can be calculated using the following equation:

\[
\text{DI}_x = \frac{\sum_{h=0}^{23} \text{GT}_x h \times \text{IR}_x h}{1000}
\]

where \(h\) = hour of the day, from 0 to 23; \(\text{DI}_x\) = daily intake, in kg DM, of herbage \(x\); \(\text{GT}_x h\) = Grazing time, in minutes, on herbage \(x\) in hour \(h\); \(\text{IR}_x h\) = the appropriate intake rate, in g DM min\(^{-1}\), of herbage \(x\) for hour \(h\); Preference can then be calculated using these herbage intakes. More detailed descriptions of the techniques used to record grazing activity can be found in Penning and Rutter (2004).

2.4. Measuring selection

Selection cannot be measured by direct manual observation, as the observer cannot tell by observation alone which herbage the animal is eating when it is grazing from an intimately mixed grass/clover sward. This problem is usually overcome using the \(n\)-alkane marker technique (Dove and Mayes, 1991; Newman et al., 1995). \(n\)-Alkanes are found in
the waxy cuticles of plants, and different plants have different ratios of \(n\)-alkanes of different chain lengths. Diet composition analysis involves collecting representative samples of the two herbage, as well as faecal samples (ideally collected at regular intervals over at least a 24 h period), and then analysing each of these for a range of \(n\)-alkanes. These data can then be processed using the software package ‘EatWhat?’ which carries out a least-squares optimisation procedure to estimate diet composition (Dove and Moore, 1996). The diet composition estimates from the \(n\)-alkane technique are based on the animals’ dry matter (DM) intake, so are equivalent to estimates based on the multiple of grazing time and intake rate (as discussed in the previous section). Whereas preference measurements based on grazing time can be used to investigate diurnal patterns of preference, this is not possible with the \(n\)-alkane technique. This is because the rumen buffers ingested herbage to such an extent that any diurnal patterns are masked, and the technique just gives an overall estimate for the composition of the diet consumed.

3. General results

The results from a range of studies investigating diet preference for grass and legumes are summarised in Table 1. All of the studies showed that sheep and cattle did not graze at

<table>
<thead>
<tr>
<th>Animal species</th>
<th>Lactating or dry</th>
<th>Herbage choice</th>
<th>% Legume</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sheep</td>
<td>Lactating</td>
<td>PG/WC</td>
<td>79.7</td>
<td>Parsons et al. (1994)</td>
</tr>
<tr>
<td>Sheep</td>
<td>Lactating</td>
<td>PG/WC</td>
<td>71.6</td>
<td>Penning et al. (1995)</td>
</tr>
<tr>
<td>Dairy sheep</td>
<td>Lactating</td>
<td>AG/Sulla</td>
<td>74</td>
<td>Rutter et al. (2005b)</td>
</tr>
<tr>
<td>Dairy cows</td>
<td>Lactating</td>
<td>PG/WC</td>
<td>70</td>
<td>Rutter et al. (1999)</td>
</tr>
<tr>
<td>Dairy cows</td>
<td>Lactating</td>
<td>PG/WC</td>
<td>78</td>
<td>Rutter et al. (2001)</td>
</tr>
<tr>
<td>Dairy cows</td>
<td>Lactating</td>
<td>PG/WC</td>
<td>73.8</td>
<td>Rutter et al. (2004a)</td>
</tr>
<tr>
<td>Sheep</td>
<td>Dry</td>
<td>PG/WC</td>
<td>65.8</td>
<td>Parsons et al. (1994)</td>
</tr>
<tr>
<td>Sheep</td>
<td>Dry</td>
<td>PG/WC</td>
<td>91.8</td>
<td>Newman et al. (1994)</td>
</tr>
<tr>
<td>Sheep</td>
<td>Dry</td>
<td>PG/WC</td>
<td>71.0</td>
<td>Harvey et al. (1996)</td>
</tr>
<tr>
<td>Sheep</td>
<td>Dry</td>
<td>PG/WC</td>
<td>88.4</td>
<td>Harvey et al. (1997)</td>
</tr>
<tr>
<td>Sheep</td>
<td>Dry</td>
<td>PG/WC</td>
<td>66.8</td>
<td>Harvey et al. (2000)</td>
</tr>
<tr>
<td>Sheep</td>
<td>Dry</td>
<td>PG/WC</td>
<td>70</td>
<td>Cosgrove et al. (2001)</td>
</tr>
<tr>
<td>Sheep</td>
<td>Dry</td>
<td>PG/WC</td>
<td>c60</td>
<td>Rook et al. (2002)</td>
</tr>
<tr>
<td>Dairy heifers</td>
<td>Dry</td>
<td>PG/WC</td>
<td>65*</td>
<td>Cosgrove et al. (1996)</td>
</tr>
<tr>
<td>Dairy heifers</td>
<td>Dry</td>
<td>PG/WC</td>
<td>68</td>
<td>Torres-Rodriguez et al. (1997)</td>
</tr>
<tr>
<td>Dairy heifers</td>
<td>Dry</td>
<td>PG/Lotus</td>
<td>70</td>
<td>Torres-Rodriguez et al. (1997)</td>
</tr>
<tr>
<td>Dairy heifers</td>
<td>Dry</td>
<td>PG/WC</td>
<td>63.9</td>
<td>Rutter et al. (2004b)</td>
</tr>
<tr>
<td>Beef heifers</td>
<td>Dry</td>
<td>PG/WC</td>
<td>60</td>
<td>Rutter et al. (2005a)</td>
</tr>
</tbody>
</table>

All the preference values quoted are from animals that had free choice of grazing from grass and legume monocultures, and had prior experience of this treatment before the start of the measurements. The data are from the first day that the measurements were recorded in each study. The figures given are the mean values across any treatment groups such that the preference represents that measured or expected when the animals are offered 50% grass and 50% legume by ground area. AG = annual ryegrass; PG = perennial ryegrass, WC = white clover.

* This is one of the 3 months studied. The preferences in the other 2 months were not significantly different from grazing at random i.e. 50:50.
random but consumed mixed diets. With two exceptions (Newman et al., 1994; Harvey et al., 1997), the animals in all the studies showed a partial preference for clover of 70 ± 10%. Of particular interest are the results from the lactating Sarda dairy ewes given a choice of annual ryegrass (Lolium rigidum, Gaudin) and Sulla (Hedysarum coronarium L.) (Rutter et al., 2005b), and those from heifers given a choice of perennial ryegrass and Lotus corniculatus (Torres-Rodriguez et al., 1997). The similarity between the preference results from these studies and those reported for perennial ryegrass and white clover shows that preference for legume versus grass is not necessarily affected by the species of grass or legume, and that the results from the white clover and perennial ryegrass trials could be applicable to a wide range of other grasses and legumes.

3.1. Diurnal pattern of preference

Both sheep (Parsons et al., 1994; Harvey et al., 2000; Rutter et al., 2005b) and cattle (Rutter et al., 2004a,b) show a consistent diurnal pattern of preference, with a strong preference for legume in the morning, but the proportion of grass in the diet increases over the course of the day (Fig. 1). This has been attributed to the proportion of the total available time spent grazing on grass increasing as the day progressed (Harvey et al., 2000).

3.2. Factors affecting preference

The proportion of clover offered influences preference, with a higher preference for clover the higher the proportion, typically in terms of ground area offered being found in

![Fig. 1. Diurnal patterns of preference for white clover (vs. perennial ryegrass) for dry and lactating ewes (Parsons et al., 1994), for lactating dairy cows (Rutter et al., 2004a), for dry dairy heifers (Rutter et al., 2004b), and of preference for Sulla (vs. annual ryegrass) for lactating Sarda ewes (Rutter et al., 2005b). The data for each line represent the mean values of treatments offering varying proportions of legume (by ground area) such that the mean proportion offered in each case was 50% grass and 50% legume. The data are from the first day that the measurements were recorded in each study. The animals were maintained on spatially separated monocultures of grass and legume for several days prior to the measurements being taken.](image)
sheep (Parsons et al., 1994), lactating dairy cattle (Rutter et al., 2004a) and dairy heifers (Rutter et al., 2004b).

Parsons et al. (1994) found that lactating sheep showed a statistically significant higher preference for clover on day 3 of their trial, with the marginal means for days 1 and 6 being in the same direction as day 3 although the difference in preference between the lactating and non-lactating (dry) ewes on days 1 and 6 were not statistically significant. Table 1 shows that, from the 18 diet preference studies reviewed, with 3 exceptions, lactating and non-lactating animals showed a preference for legume of $75 \pm 5$ and $65 \pm 5\%$, respectively. These results indicate that lactating animals generally show a higher preference for legume than non-lactating animals, although this needs verification through further research. Sheep that have been fasted show a lower preference for clover than those that have not (Newman et al., 1994). The relative availability of clover also affects the proportion of clover in the diet, with a decline in clover in the diet as the relative availability of the clover declines (Harvey et al., 2000; Rook et al., 2002). Preference for clover may also vary with season (Cosgrove et al., 1996).

4. Why do ruminants eat mixed diets?

The similarities in the preference of sheep and cattle for legumes and grass (including diurnal patterns and the fact that they both consume mixed diets) suggest that a common biological basis underpins dietary preference in both animal species. Various theories have been proposed to account for the nature of this possible common biological basis, and are discussed below.

4.1. Discounted theories

Poor spatial memory (i.e. being unable to remember the location of grass and clover patches) does not appear to be a plausible explanation for mixed diets in ruminants as both sheep (Edwards et al., 1996) and cattle (Laca, 1998) have been shown to possess good spatial memory. Discrimination error has also been proposed as a possible explanation for mixed diets (Illius et al., 1999). However, discrimination error due to poor visual or olfactory acuity also appears to be an implausible explanation for mixed diets for sheep as Edwards et al. (1997) demonstrated that they can learn to discriminate between turfs of grass and clover that are presented behind a mesh i.e. they can discriminate between grass and clover by sight and smell alone. Although the visual acuity of cattle (Piggins and Phillips, 1996) is less than that of sheep (Entsu et al., 1992), the similarities in diet preference between the two animal species suggests that visual acuity is also unlikely to be a credible explanation for mixed diets in cattle. However, further research is needed before this can be categorically ruled out in cattle.

Intake rate maximisation has also been proposed as a possible explanation for mixed diets. The fact that both sheep (Penning et al., 1991) and cattle (Rutter et al., 2004a) can eat clover more quickly than grass, suggests that they are failing to maximise their rate of intake as they are incorporating grass, which has a lower intake rate, into their diets. ‘Matching’ which, in the context of a grazing herbivore, describes the correspondence
between the relative intake rates of the feeds available and their proportion in an
animal’s diet, has also been proposed as an explanation for mixed diets (Senft et al.,
1987). When applied to the foraging behaviour of individual animals, matching only
refers to allocation of time spent foraging between two depleting alternatives, when it is
the rate-maximising strategy (Illius et al., 1999). However, grazing preference trials
have shown that goats (Illius et al., 1999) and dairy cattle (Rutter et al., 2004a)
considerably over-match, and so matching does not appear to be a plausible explanation
for mixed diets in free-ranging ruminants.

4.2. Current theories

In addition to the discounted theories there are a number that are still current i.e. have
yet to be disproved. These are discussed in the next six sub-sections.

4.2.1. Novelty

Parsons et al. (1994) showed that sheep show a stronger preference for the herbage
previously lacking in their diet, although this effect diminished after 11 h. Rutter et al.
(1999) demonstrated that mixed diets and a partial preference for clover were maintained
for at least several weeks in long term studies with dairy cattle, so although novelty plays a
role in the short-term (i.e. hours), it cannot explain why ruminants eat mixed diets in the
long term (i.e. weeks).

4.2.2. Sampling

A theory commonly proposed to account for mixed diets is that animals need to
‘sample’ dietary options in order to assess the relative quality of the different feeds
available (Dumont and Gordon, 2003). Whilst the natural pastures in which ruminants
usually forage can show a high degree of spatial heterogeneity in terms of their quality, the
spatially separate, pure monocultures offered in preference studies provide the animals
with a far simpler and more clear-cut choice, with comparatively clear quality differences
between two highly contrasting forages. So, whilst sampling has value in natural pastures
where quality differences are rarely clear cut (Dumont and Gordon, 2003), its value is
questionable in the separate monocultures used in preference trials. The importance of
sampling was also questioned by Harvey and Kelly (1997) who showed that sheep foraging
from bowls containing either pelleted, nutritionally improved straw or molassed lucerne
ate monospecific diets i.e. they did not need to sample continuously from the foraging
options available to them. These findings undermine the theory of sampling as an
explanation of mixed diets. However, it could be that domestic ruminants have evolved
foraging strategies based on ‘sampling’ as a result of thousands of years of evolution of
foraging from naturally patchy environments, and continue to apply this strategy even
when grazing in an environment that offers a clear quality contrast (e.g. choice from
monocultures). However, this hypothesis requires investigation.

4.2.3. Maintaining rumen function

Another evolutionary-based theory to account for mixed diets in ruminants is that the
animals need to maintain some grass in their diets in order to maintain effective rumen
micro-flora and fauna (Rutter et al., 2000). Although sheep (Orr et al., 1997) and cattle (Orr et al., 2004) can successfully live on clover-only diets (low in fibre compared with grass), this is likely to lead to a change in their rumen micro-organisms such that their ability to digest fibre is likely to be less than that of animals that maintain grass in their diets. Whilst this has few implications for a modern, managed domestic ruminant, evolution would have favoured those animals that maintained a more diverse rumen micro-flora and fauna, as this would have given them an increased ability to cope with environmental change when e.g. the availability of low-fibre plants became restricted compared with the fibre-rich grasses. Again, this theory remains untested, and warrants investigation.

4.2.4. Carbon and nitrogen balance

One obvious difference between grass and clover is that they differ in the relative proportions of the nutrients that they contain. Two important dietary components are carbon (C) and nitrogen (N), which are important for energy and protein synthesis, and white clover has a higher proportion of N in relation to C than grass (Whitehead, 1995). Balancing the C and N content of the diet is important, as eating a diet too rich in N will have implications for the animal’s energy budget, as extra energy will need to be expended by the animal to process any excess N that has been ingested, digested and absorbed. It is unlikely that a single plant species will have the perfect balance of nutrients to meet an animal’s nutritional needs, and so the animal will need to select a variety of plant species in order to achieve a diet that provides an optimum balance of nutrients. There will have been strong evolutionary pressure for ruminants to adopt diet selection strategies that optimise their intake of nutrients, especially C and N, as the energetic costs associated with getting it wrong would have placed them at a competitive disadvantage compared with more efficient foragers.

In non-ruminant animals, diet selection and intake appear to be governed by their attempt to meet their ideal protein intake (Kyriazakis, 2003). Studies have shown that ruminants are capable of selecting a diet that meets their protein requirements when given a choice between two concentrated feeds that differ in their protein contents (Kyriazakis and Oldham, 1993; Kyriazakis et al., 1994). This led to the proposal that ruminants select diets based on the rumen degradable protein (RDP) content on the feedstuffs available (Kyriazakis et al., 1999). However, these studies have generally used housed animals fed either concentrate or silage diets, and the role of the N concentration of the diet (which includes N from RDP) selected by grazing ruminants is less clear, as studies with grazing ruminants have failed to show any effect of grass N concentration on the preference for clover (Harvey et al., 1996; Cosgrove et al., in press). Whilst this could be seen as evidence that N concentration does not play a role in diet selection at grazing, this is not necessarily the case. This is because an animal faced with a choice between high-N clover and a high-N grass cannot select a forage that will allow it to dilute the N concentration of its diet. Consequently, it may as well do what it usually does when offered high-N clover and low-N grass i.e. eat a mixed diet consisting of ~70% clover. Cosgrove et al.’s (in press) study does, however, provide some evidence to support the hypothesis that diet selection is linked to N concentration. They showed that sheep offered a choice between low-N and high-N grass choose a mixed diet consisting of 77% high-N grass i.e. they appeared to be selecting a mixed diet from grass swards where the main contrast was in N concentration only. There is
also further empirical support for the hypothesis that diet selection is linked with the animal’s C:N balance. Merry et al. (2002) studied the microbial protein synthesis in an artificial rumen given different proportions of ryegrass and red clover silages. They found that the optimum level of microbial protein synthesis was achieved with 70% legume and 30% grass i.e. in the middle of the range of preference for clover shown by grazing ruminants. This supports the hypothesis that ruminants eat mixed diets in order to balance the supply of nutrients (principally C and N) to the rumen so as to optimise the efficiency of microbial protein synthesis. If this hypothesis is correct, it will have major implications for improving the efficiency of production on-farm by utilising grazing management strategies that facilitate diet choice by livestock. This could bring economic and environmental benefits, which are discussed in Section 5, and so clearly warrants further research.

4.2.5. Conditioned taste aversion

Plants have evolved a range of toxins that produce negative post-ingestive consequences in the herbivores that eat them, causing the animals to develop a taste aversion to those plants (Provenza, 1995). Such acquired aversions have been proposed as a basis for mixed diets in free-ranging herbivores (Provenza, 1996), and there is some empirical evidence to support this. Sheep that have been fasted show a lower preference for clover than non-fasted sheep (Newman et al., 1994), even though they can eat clover more quickly than grass. It is possible that the sheep have learnt that the rapid ingestion of a large quantity of clover can lead to bloat (ruminal tympany), and so they dilute their diet with grass to avoid this condition. This could also explain the diurnal pattern of preference for legumes, as the animals might have learnt to gradually increase the proportion of grass in their diet as the day progresses to help dilute the build up of toxins from the legume. The role of conditioned taste aversion in diurnal patterns of preference has some support from a study into the preference for Sulla and annual ryegrass (Rutter et al., 2005b). The researchers found that the diurnal pattern of preference for Sulla declines more rapidly than that reported for white clover, but then recovers in the early afternoon, before declining again (Fig. 1). It was proposed that this could relate to the comparatively high levels of condensed tannins in Sulla (cf. white clover) having an anti-nutritional effect causing the animals to switch to grass earlier in the day in order to dilute the Sulla in the rumen.

If conditioned taste aversion and bloat do play a role in diet selection, one might expect that treatment with an anti-bloat agent would affect preference. However, this appears not to be the case, as Rutter et al. (2004b) found no differences in the diet selected or bloat levels in dairy heifers with and without an anti-bloat treatment. However, the animals in their study had had at least 7 days prior exposure to clover, so could have learnt a conditioned taste aversion over that period and consequently to adopt a mixed diet with which they continued during the study period. Again, further research is needed to explore the role of conditioned taste aversions in mixed diets in ruminants.

4.2.6. Anti-predator behaviour

Sheep and cattle are described as crepuscular i.e. show peaks in foraging activity at dawn and dusk (Fraser, 1983; Albright and Arave, 1997, p. 22). In temperate regions, sheep (Champion et al., 1994; Gluesing and Balph, 1980) and cattle (Gibb et al., 1998) generally avoid grazing at night, and the major periods of eating in feedlot bulls are associated with
sunset and sunrise, shifting with seasonal changes, with little eating occurring at night (Gonyou and Stricklin, 1984). In general terms, daily periods of inactivity can be for digestion, energy conservation or predator avoidance (Manning and Dawkins, 1992, p. 73). The presence of bright moonlight has been shown to result in an increase in the proportion of grazing that occurs at night, both in dairy cows (Vilela et al., 1974) and buffaloes (Somparn, 2004), suggesting that the lack of grazing at night is in some way directly related to low light levels, and therefore not related to the needs of digestion or energy conservation per se. Whilst it is possible that the lack of grazing in low light levels is simply due to the fact that the animals cannot see sufficiently well to move about and select their diets, it is also possible that it is a predator avoidance strategy. Lima and Dill (1990) argue that predation has been a major selective force in the evolution of animals, in both evolutionary and ecological time (i.e. during the lifetime of an animal), and demonstrated that the presence of predators can effect foraging behaviour. For example, the presence of predators causes fish to spend more time concealed and so leads to a reduction in their nutrient intake (Gilliam and Fraser, 1987). Wild African ungulates face a very real risk of being attacked by predators, and this could explain why they forage in multi-species groups (Sinclair, 1985) and avoid habitats with dense cover that could hide predators (Underwood, 1982). Jarman and Jarman (1973) found that wild impalas restrict their mobile activities to the daytime, with their one period of nocturnal grazing coinciding with the time of least predator activity. There is also some limited evidence that the behaviour of domestic livestock is affected by predation risk. Gluesing and Balph (1980), found that coyotes killed domestic lambs that were more active, and they suggested that, when domestic sheep are subject to night-time attacks from coyotes, they may restrict vulnerable activities, such as grazing, to the daytime. Penning et al. (1993) showed that daily grazing time was reduced as group size in grazing sheep was reduced, which they attributed to the need for increased vigilance as group size reduced. Although most domesticated sheep and cattle are usually protected from predators, and their domestication has lead to a reduction in anti-predator responses (Mignon-Grasteau et al., 2005), they still exhibit some predator-avoidance strategies that are similar to wild animals (Dwyer, 2004; Boissy et al., 2005).

In order to avoid grazing at night, an effective strategy for the animal would be to eat a bulky feed rich in fibre with a low rate of passage (i.e. grass) in the evening, helping to maintain rumen fill and reducing the need to eat to maintain rumen fill at night. This hypothesis has some support from diet preference work with sheep given a choice of vegetative and reproductive grass swards (Dumont et al., 1995). In these studies, sheep showed a diurnal pattern of preference in which the preference for the reproductive sward increased in the evening. These reproductive swards had a higher crude fibre content than the vegetative swards, supporting the hypothesis that the sheep seek a diet with a higher concentration of fibre in the evening. This study also helps to discount an alternative explanation of the diurnal pattern of preference for clover and grass, which is based on diurnal changes in water soluble carbohydrate (WSC) levels. Cattle can discriminate between hay cut in the morning and in the afternoon, and they prefer that cut in the afternoon (Mayland et al., 2000). WSC levels increase over the course of the day in grass (Orr et al., 2001) but this is not the case in clover (Orr et al., 1997), and so the diurnal pattern of preference may simply reflect the fact that grazing ruminants prefer the grass in
the afternoon and evening because it is sweeter. However, Dumont et al. (1995) showed that sheep appear to target fibre in the evening and not WSC, which is in keeping with the hypothesis that the diurnal pattern of preference for grass and clover in ruminants is associated with anti-predator behaviour.

4.3. Summary of current theory

Of the possible explanations for mixed diets discussed above, the latter two (conditioned taste aversion and anti-predator behaviour) might at first appear to be the most attractive as these explain both mixed diets and diurnal patterns of preference. Whilst this may appear as justification to discount the first four (novelty, sampling, C/N balance and maintaining rumen function), as they do not account for the diurnal pattern of preference, it is possible that more than one (and possibly all six) of these explanations are valid. That is, the animal may be selecting a diet in order to achieve a balance between a number of different, possibly competing goals, and it is not necessarily the case that mixed diets have a single common basis underpinning them. For example, in hot weather cattle will spend a greater proportion of their time grazing at night (Weaver and Tomanek, 1951), and this could be due to them having to trade-off the risk of suffering heat stress if they forage during the day against the risk of predation if they forage at night, or the risk of starvation if they avoid foraging both during the day and at night.

The possibility that the animals might be adopting a multiple-goal diet selection solution needs to be taken into account by researchers studying the basis of diet selection when designing experiments. The idea that animals may be making trade-offs between different, possibly competing, goals when determining the diets they select has implications for the practical exploitation of this work, and this is discussed in the next section.

5. Practical implications and applications

The research discussed so far has largely been focussed on improving our scientific understanding of the factors affecting preference, and so has looked at diet choice in animals offered the two herbages as spatially separate monocultures. However, it is usually the case, under current agricultural practice, to graze grass and clover as an intimately mixed sward. This imposes a constraint on foraging, because it requires the animals to search through the mixture looking for their preferred herbage at that point in time i.e. it is selection (as defined in Section 2.1), and this may impose a cost to that animal that may influence the efficiency with which it acquires nutrients. This, in turn, could have implications for both production and the environment, and these are discussed below.

5.1. Selection costs

Champion et al. (2004) studied grazing time and intake in groups of sheep grazing swards under four different treatments: grass only, clover only, an intimately mixed grass/clover sward and free choice between adjacent grass and clover monocultures. They found that the highest daily herbage intakes were from the adjacent monocultures, and the lowest
daily intake (despite having the highest daily grazing time) was from the mixed sward. Similar results were also reported by Cosgrove et al. (2001). These studies clearly demonstrate that there are selection costs associated with grazing a mixed sward, and that, purely in terms of intake, it is a detrimental move from using pure ryegrass swards. The studies also demonstrate that intakes can be increased by offering grass and clover as separate swards (cf. grass or clover only), and that this could have potential application on-farm to increase production.

5.2. Production benefits

Whilst the studies of Cosgrove et al. (2001) and Champion et al. (2004) did not look for any production benefits arising from the increased intakes associated with grazing sheep on grass and clover as separate monocultures (compared with an intimately mixed grass/clover sward), production benefits have been demonstrated in dairy cattle. Nuthall et al. (2000) showed that, under continuous stocking in the United Kingdom, cows given free choice to graze adjacent clover and grass monocultures (offered at a ratio of 2:1 clover:grass by ground area) produced 12.0% more milk than cows grazing an intimately mixed sward. Cosgrove et al. (2001) reported a 11% increase in milk yield in a similar experiment conducted in southwest Victoria, Australia. Rutter et al. (2001) then showed that continuous free-choice is not necessary to achieve the production benefits arising from grazing adjacent grass and clover. They used a treatment called ‘Temporal Allocation’ in which the cattle grazed clover (only) between morning and afternoon milking and then grass (only) between afternoon and morning milking (i.e. roughly mimicking their diurnal pattern of preference as described earlier). They found that there were no differences in the daily dry matter intake or milk yield between the cows on the temporal allocation treatment and those offered continuous free-choice between adjacent grass and clover. This demonstrated that free choice is not necessary for boosting production by grazing grass and clover separately. Rutter et al. (2003) found that under rotational grazing with a twice-a-day allocation of fresh herbage, cows under a Temporal Allocation treatment (receiving an allocation of fresh clover after morning milking and fresh grass after afternoon milking) produced 14.6% more milk than cows receiving a twice-a-day allocation of a fresh mixed sward.

The production benefits achieved from grazing grass and clover as separate swards are likely to be at least in part achieved from higher daily intakes, as demonstrated by Nuthall et al. (2000) and Rutter et al. (2003). However, the production increases could also result from an improvement in feed conversion efficiency, with the animal optimising the ratio of C and N in its diet, as discussed in Section 4.2.4. As well as having production and economic benefits for the farmer, improved efficiency of production could also have environmental benefits, and these are discussed in Section 5.4.

5.3. Achieving separation

The studies into diet preference reviewed in this paper have invariably achieved separation of the grass and clover by sowing a large, contiguous part of the field with one species and the remaining part of the field with the second i.e. one area of grass and one
area of legume per paddock. Whilst this is appropriate for a scientific study on diet preference, it is probably not the most efficient arrangement for optimising all the potential benefits of novel grass/legume grazing management systems on-farm. One important potential problem from a practical point of view is that a large spatial scale of separation of grass and clover is likely to reduce one of the major benefits of incorporating clover into grass swards i.e. the transfer of N from the clover to the grass. However, this is not as big a problem as it first appears, as the majority of the N transfer from clover to grass occurs via the animal’s dung and urine (Ledgard, 1991), although increasing the spatial scale of separation probably reduces the below-ground transfer of N. Rutter et al. (2005a) looked at preference in beef cattle offered grass and clover sown in adjacent strips of widths of 108, 36 and 12 cm and a mixed sward. They found that cattle select ~60% clover from the two wider strips (108 and 36 cm) but ~37% from the 12 cm strips and the mixed sward, indicating that the critical spatial scale of separation for reducing the selection costs in cattle is between 36 and 12 cm. Whilst further research is needed to further refine this critical spatial scale, it is clear that the benefits of separation could be achieved on-farm at a relatively fine spatial scale (36 cm or less), and that field scale separation is not necessary. This finer spatial scale has the potential to offer better below-ground N transfer than field scale separation, although this requires further research. Although separation at the critical scale could be achieved on-farm by sowing strips of grass and legume, it might also be achieved by changing the selection criteria used by grass and legume breeders. That is, strains of grass and legumes could be selected to grow with a ‘naturally’ patchy habit of the appropriate spatial scale. This could remove the need to sow in strips and might overcome the problem found with current commercial strains of grass and clover i.e. that they tend to grow into each other such that the separate strips deteriorate into a mixed sward over several years.

5.4. Environmental benefits

Diet choice could have an important role in achieving environmental benefits in two ways. Firstly, if the production benefits of grazing grass and clover as separate swards are due, at least in some part, to an increase in the efficiency of capture of nutrients, then this approach could be used to improve the product:pollution ratio from grazing livestock. That is, it could be used to increase unit production (e.g. kg milk, beef or lamb) per unit pollution, resulting in less environmental pollution, especially diffuse nitrate pollution, from livestock agriculture. High feed conversion efficiencies are also associated with reduced methane emissions (DeRamus et al., 2003), so giving another potential environmental benefit of this approach i.e. reducing greenhouse gas emissions from grazing ruminant livestock. Further research is needed to explore the relationships between diet preference, nutrient capture efficiency and pollution from novel grazing management systems based on grazing spatially separate grass and clover.

The second way in which diet choice is likely to play a role in achieving environmental benefits is through the increased use of the grazing animal as a tool to promote and maintain plant (and dependent animal e.g. insect and bird) biodiversity (Rook et al., 2004). The scientific research summarised earlier in this paper demonstrates that grazing livestock have clear diet selection goals, and these need to be taken into account if we
are to develop grazing management strategies that maintain and promote biodiversity. However, further research is needed to look at diet selection in complex, botanically rich, biodiverse swards. These swards not only offer a much wider range of choice of plant species than the simple, two-species choices studied to date, but they also have a high degree of spatial heterogeneity (Hofmann and Tallowin, 2004). Research is needed to look at multi-species plant choice, as well as the effects of different scales of spatial heterogeneity on diet selection.

As discussed earlier, various factors influence diet preference, and the use of animals to which specific plants are either novel or familiar, or animals of different physiological states (e.g. lactating versus dry) could be used as part of a grazing management strategy that uses differences in the animals’ diet preferences to achieve desirable biodiversity goals. Whilst further research is needed to improve our scientific understanding of the complex interactions between preference and the spatial scale of heterogeneity in multi-species swards, the use of e.g. either dry or lactating animals in grazing management should provide a relatively practical approach that could be adopted by practitioners in the field. The role of the grazing animal in maintaining and promoting biodiversity would be further enhanced if diet preference could be manipulated in some way, such that animals could be persuaded to eat a particular range of plants, but not others, that would help achieve a particular biodiversity goal. Although, as we have seen above, there are a range of factors that affect diet preference and selection, there have not yet, to the author’s knowledge, been any systematic attempts to alter preference with this specific aim. If, as was discussed earlier, the animal’s diet choice is a trade-off between different, possibly competing goals, there is likely to be more scope for manipulating diet preference than if the animal’s diet choice is based on achieving a single goal. This is because it is more likely that the balance in a trade-off between different goals can be shifted more readily than shifting the animal’s focus from a single goal. One possible manipulation to change diet choice would be to form conditioned taste aversion associations (Provenza, 1995) for plants that were not to be eaten. However, this approach would be very labour intensive, as each animal in a herd or flock would have to receive taste aversion training, and there would be ethical implications for the widespread use of such aversive training. Consequently, the practical and ethical problems of using conditioned taste aversion in grazing management to promote biodiversity would probably mean it is unlikely to be widely adopted by practitioners.

6. Summary

Grazing sheep and cattle given a free choice between adjacent grass and clover monocultures eat mixed diets with a partial preference for clover of approximately 70%. There is a diurnal pattern of preference, with a stronger preference for clover in the morning. Various theories have been proposed to account for the fact ruminants eat mixed diets, and those with an evolutionary basis (i.e. balancing nutrient intake, maintaining rumen function, sampling, avoiding toxins and avoiding predators) warrant further research, especially to determine if the animal is making one or more trade-offs between more than one of these goals. Grazing grass and clover with a degree of spatial separation
reduces the costs of selection to the animals, and could be used to increase livestock production on-farm. Further research is needed to look at diet choice in ruminants grazing botanically diverse swards before practical recommendations can be given for using grazing to promote biodiversity in semi-natural grasslands.

7. Conclusion

Although proximate studies show grazing sheep and cattle eat mixed diets, have a preference of 70% for clover and can achieve higher daily intake from spatially separate grass and clover (i.e. with reduced selection costs), further research is needed to understand the ultimate basis of mixed diets in ruminants.

References


