THE UNDERWOOD LECTURE

PASTURES AND GRAZING ANIMALS - THE INTERACTION CONTINUES

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HISTORICAL INTRODUCTION

It is in the nature of things that there will come a time when the Underwood Lecturer can no longer claim some close assocation with Professor Eric Underwood. My recollection is that I met Underwood only twice, once when I was a post-graduate student, and again some years later after I had joined CSIRO. Nevertheless, Underwood's contributions to animal science were such, particularly in relation to the nutrition of grazing animals, that he profoundly influenced both his own generation and subsequent generations of animal nutritionists in Australia, including mine.

Underwood's first publication (Underwood 1929) was concerned with the nutritive value of pastures in Western Australia. It was also the first scientific publication by the University of Western Australia (see Blaxter 1981) and, as we were reminded in the first Underwood Lecture (Moir 1984), it opened with the words: " No apology need be made for the subject of this enquiry in a State such as Western Australia, where economic prosperity depends so largely on the productivity of flocks and herds..."

In the ensuing 70 years, much has changed in the structure of the rural and total economies in Australia, but the general sentiment of Underwood's opening words is as true today as it was in 1929. Indeed (and by coincidence), a variant of Underwood's words introduces a recent discussion of the constraints to the modelling of plant/animal interactions (Dove 1996a) as follows:

"The interaction of grazing animals with their pasture ultimately determines the profitability of grazing enterprises...so that the processes of diet selection and intake assume major economic importance."

In the 18 years following his first publication, Underwood produced a further 44 publications and in 1946 was appointed to the Hackett Chair of Agriculture in the University of Western Australia. By this time, grazing experiments had already commenced at the CSIRO Dickson Experiment Station in Canberra (Station Overseer's Diary 1946), and in 1947 the CSIRO Regional Pastoral Laboratory (ultimately 'Pastoral Research Laboratory') came into being at Chiswick, near Armidale, NSW. In that same year, the 1998 Underwood Lecturer also came into being. By 1965, a further 18 years later, Underwood had produced an additional 45 publications, Dickson Experiment Station had been replaced by Ginninderra Experiment Station, and both Ginninderra and Chiswick were well established as Australian centres making major contributions in the study of the relationships between animal performance and pasture conditions. The 1998 Underwood Lecturer had also just commenced an Agricultural Science degree at the University of Melbourne.

The two decades after Underwood's appointment to the Hackett Chair were those in which the use of superphosphate, the control of rabbits and the realisation of the importance of stocking rate were productive research areas which made major economic contributions to Australian agriculture (for details, see Lloyd Davies and Myers 1985). In the 20 years from 1965, the increasing availability of computing power allowed the conduct of detailed studies on components of grazing systems, with the hope of combining these in computer simulations of the whole system. In effect, the work conducted at Canberra, Chiswick and at other Australian sites increasingly sought to elucidate the processes involved in the interactions between animals and pastures, and to allow the nutrition of grazing animals to be managed with a similar degree of certainty to that of housed or hand-fed animals.

It would be presumptious of me to make any further attempt to chart the history of animal nutrition work in Australia, since this has been discussed by others who are more qualified so to do (see Lloyd Davies and Myers 1985; McDonald 1988; Corbett and Ellis 1997). Moreover, it is not my aim in this lecture to present a review in fine detail of the many ways in which grazing animals interact with their pasture. These have been discussed in recent reviews such as Dove (1996a) and the chapters in Hodgson and Illius (1996). Rather, this lecture will take, as examples, the development of several specific areas of research on plant/animal interactions and, where appropriate, relate these developments to the mineral nutrition of livestock, the area in which Underwood made such major contributions.

The examples to be considered can be put in the terms of the following questions.

1. How much herbage does the grazing animal consume and, compared with the herbage on offer, what is the composition of the consumed diet (in terms of both nutrients and plant species)?
2. What is the nature and quantity of the products of digestion, compared with the animal's nutrient requirements?
3. Are supplements required to make good shortfalls in nutrient supply, and to what extent will substitution between herbage and supplement diminish the response to supplementation?
4. Can the nutritional interactions between grazing animals and herbage be monitored closely enough to estimate the flows of toxic materials through or from the grazing system?
5 Can the processes involved in the interactions between soils, pastures, supplements and animals be represented in sufficiently accurate mathematical terms as to be algorithms within models of nutrient cycling in grazed pastures?

In his own research, Underwood was principally though not exclusively concerned with the mineral nutrition of livestock and the exploration of questions 1 to 3 above, as they related to frank mineral deficiencies. He was acutely aware of the degree to which grazing animals, especially sheep, could consume a diet different from the average of that on offer, and commented that herbage samples "...as collected and analysed may not represent the material actually eaten by the animal. Animals exhibit marked preferences for different types and parts of plants...Selective grazing could therefore greatly influence actual mineral intakes by animals." (Underwood 1966).

WHAT DO ANIMALS EAT, AND HOW MUCH?

One of the key variables determining animal production is the amount of pasture consumed by an animal. In part, this accounts for the effort devoted to the development and use of techniques to estimate herbage intake but, as discussed elsewhere (Langlands 1987; Dove and Mayes 1991), the extent of research effort is also a reflection of the difficulty of measuring diet composition and herbage intake.

Under Australia's extensive grazing systems, herbage intake has been estimated most often by exploiting the relationship between intake, digestibility (or more correctly, indigestibility) and faecal output since, with minimal disturbance, this approach can give an estimate spanning several days and can also provide some indication of between-animal variability. Until the late 1980s, faecal output and herbage digestibility were estimated separately, the former from the dilution of chromium sesquioxide (Cr_2O_3) administered as an external marker and the latter from *in vitro* digestibility estimates on herbage samples collected by oesophageally-fistulated (OF) animals. Intake was then estimated from the equation

$$\text{Intake} = (\text{Faecal output})/(1 - \text{digestibility})$$

Further details of the use of the Cr_2O_3/*in vitro* approach can be found elsewhere (Langlands 1987; Dove and Mayes 1991, 1996; Corbett and Ellis 1997). Of the possible sources of error, the most potent are those relating to the collection and analysis of the OF samples (Langlands 1987; Dove and Mayes 1991, 1996). Three types of potential error can be distinguished.

1. The relationship between *in vitro* and *in vivo* digestibilities, often established with mature animals fed near maintenance, may not apply to the test animals.
2. Only a single digestibility value is obtained, but is applied to all test animals regardless of the level of their herbage and/or supplement intake.
3 Individual test animals may consume a diet which differs in digestibility from that consumed in a single grazing by the OF animals.

In general, the last of these has been regarded as the greatest cause for concern, since it is the least controllable by the researcher. However, there can be no doubt that data of great scientific and practical importance have been obtained using this approach, and it is important to realise that these are potential and not inevitable errors. Nevertheless, newer techniques based on plant wax components can provide an estimate of diet composition and herbage intake, while at the same time avoiding these errors (Dove and Mayes 1991, 1996). Indeed, the need for OF animals may be obviated altogether.

Using plant wax components to estimate diet composition and herbage intake

Given Underwood's immense contributions to our understanding of the mineral nutrition of livestock. it is perhaps one of the ironies of science that it was another mineral nutritionist, N.D. Grace, who first suggested the possible use of a cuticular wax component (in his case, long-chain fatty acids) as a marker in herbage intake work (Grace and Body 1981). Following on from this, R.W. Mayes and colleagues suggested using a combination of dosed and cuticular wax alkanes (which are more easily analysed than long-chain fatty acids) as the basis for estimating herbage intake (see Mayes *et al.* 1986). The so-called 'alkane method' has now been validated extensively and used to estimate herbage intake in a wide range of herbivores (see Dove and Mayes 1991, 1996).

A major extension of the alkane method for estimating intake, and a feature which sets it apart from previous methods, is its capacity to provide an estimate of the botanical composition of the diet as well as an estimate of the total intake. Since pasture species differ in their pattern of cuticular alkanes, as to a lesser extent do their component plant parts, the pattern of alkane concentrations in the faeces of grazing animals can be used to estimate diet composition in terms of plant species and/or plant parts (Simpson *et al.* 1993; Simpson and Dove 1994; Dove and Moore 1995). In turn, this allows a convenient means of comparing the extent to which OF samples might differ in botanical composition from that of the herbage on offer, or the diet selected by plot sheep. To avoid the confounding effect of having two types of animal (OF and 'plot'), these comparisons can be made in the OF animals themselves (Table 1).

In the animals grazing the clover-dominant pasture, there is a general similarity between their diet selected over a week, the sample of herbage which they selected at a single grazing and the botanical composition of the sward. In this case, the OF sample would have been representative of the botanical composition of the consumed diet. By contrast, animals grazing the ryegrass-dominant pasture consumed a diet of similar botanical composition to the sward, but the OF sample collected at a single grazing was markedly different from that consumed diet. The use of herbage and faecal alkane concentrations has thus allowed the quantification of the extent of possible error which arose from the use of the second set of OF samples as if they represented the botanical composition of the consumed diet.

It is important to specify the exact nature of this error. If the aim is to obtain, using OF animals, a sample of the 'consumed diet' for use in an *in vitro* estimate of digestibility, then at least in vegetative swards in spring the difference in the botanical composition of the OF sample and the diet of the test animals may not matter. The digestibilities of these samples could be similar, resulting in only small errors when used as part of a Cr/*in vitro* estimate of intake. The problem is that one does not know whether this is the case.

However, if the OF sample is being used to obtain the C31 or C33 alkane concentrations in the 'consumed diet', for use in alkane-based estimation of intake, then the intake estimates are likely to be incorrect if the OF

Table 1. Comparison of the botanical composition (% DM) of clover-dominant or grass-dominant pastures with the botanical composition of the diet selected by oesophageally-fistulated (OF) sheep at a single grazing, or by the same sheep over a period of seven days

	Subterranean clover	Sorrel	Yorkshire Fog Grass	Perennial Ryegrass	Other
Clover dominant					
Herbage 26 Oct.	69.9	22.5	0.9	2.8	3.8
OF sample 22 Oct.	84.3	8.8	3.5	0	3.4
Diet 14-20 Oct.	91.5	5.1	0	0.8	2.6
	Phalaris	Sorrel	Soft Brome Grass	Perennial Ryegrass	Other
Grass dominant					
Herbage 18 Oct.	11.1	13.4	3.3	71.4	0.9
OF sample 22 Oct.	72.8	8.6	2.4	16.3	0
Diet 14-20 Oct.	4.3	2.8	7.9	70.4	14.7

Six animals on each pasture. Botanical composition of herbage by hand-sorting; botanical composition of OF samples and of the diet estimated from the pattern of alkane concentrations in herbage components, OF samples or faeces samples (bulked over the period shown). Calculations performed using EatWhat procedure of Dove and Moore (1995).

sample has a different botanical composition from the actual consumed diet. As discussed elsewhere (Dove and Mayes 1991, 1996; Dove and Simpson 1997a), the way around this problem is first to estimate the diet composition of the test animals and then to use the implied diet alkane concentrations to estimate herbage intakes. This also obviates the need for OF animals, which on 'animal ethics' grounds alone, must be regarded as a major advantage of this approach.

WHAT NUTRIENTS DOES THE RUMINANT GAIN FROM CONSUMED HERBAGE?

The singular feature of domestic herbivores such as sheep and cattle is the extent to which their ruminant mode of digestion ultimately provides for absorption, a mix of nutrients quite different both qualitatively and quantitatively from the nutrient composition of the consumed herbage. Faichney (1996) has discussed historical aspects of the development of marker-based techniques for studying nutrient kinetics in the ruminant, in a publication in honour of the work of R.H. Weston and J.P. Hogan, whose fruitful collaborations in the 1960s and 1970s provided a quantitative basis for predicting nutrient supply to the ruminant animal from a knowledge of the nutrient composition of the consumed diet.

Estimating nutrient supply in grazing animals

In order to estimate the amounts of key nutrients actually being presented for absorption in grazing animals, it is necessary:

(a) to provide a robust and accurate means of infusing the markers which permit estimates of the flow of the particulate and liquid phases of digesta, and thence the nutrients in digesta, and
(b) to obtain intermittent samples of digesta (usually from the rumen and the duodenum or abomasum) which are representative of the total daily flow.

The infusion of digesta-flow markers has been achieved succesfully under field conditions using portable infusion pumps (eg Corbett and Pickering 1983; Dove *et al.* 1988; Dove and Milne 1994), the development and use of which has recently been described in detail (Corbett and Ellis 1997). Digesta sampling is complicated by the existence of marked circadian variation in digesta flow under field conditions (eg Corbett and Pickering 1983; Dove *et al.* 1988). Dove *et al.* (1988) demonstrated that when expressed relative to the time of sunset, Fourier curves describing this circadian variation in lactating ewes grazing perennial ryegrass in Scotland were remarkably similar (Figure 1) to those for dry sheep grazing the same species at Armidale, Australia (Corbett and Pickering 1983).

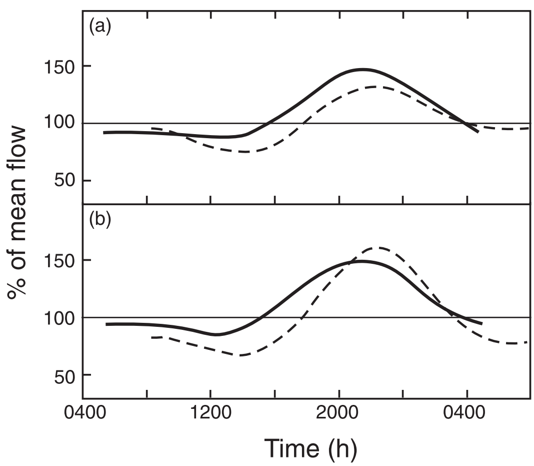

Figure 1. Fitted Fourier curves describing the circadian variation (% of mean flow) in the flows of (a) OM or DM and (b) total nitrogen (N) in the particulate phase of digesta of lactating ewes (solid lines: Dove *et al.* 1988; OM basis) or dry sheep (broken lines: Corbett and Pickering 1983; DM basis) grazing perennial ryegrass pastures. Adapted from Dove *et al.* (1988) with the kind permission of the *British Journal of Nutrition*

From their mathematical analysis of the circadian variation in digesta flows, Dove *et al.* (1988) estimated that a typical sampling schedule of 0900, 1300, 1700 and 0900hours the following day would have resulted in 7 to 10% under-estimates of actual digesta flows, confirming that attention to the sampling schedule is required in order to obtain digesta samples which are representative of total digesta (Faichney 1980).

Combining nutrient supply and herbage intake estimates

For estimates of nutrient flows in digesta to be related back to pasture conditions (and thus pasture management), they have to be related to the intake of nutrients from pasture. In turn, this implies a knowledge of herbage intake and the nutrient composition of the consumed diet, and emphasises the importance of obtaining accurate estimates of both of these. In lactating ewes grazing perennial ryegrass, Dove *et al.* (1990) calculated herbage intakes from faecal outputs combined with herbage digestibilities estimated either by *in vitro* analyses of OF samples or by using herbage and faecal concentrations of C35 alkane (Table 2). As a consequence of significant differences between these two estimates of digestibility (Dove *et al.* 1990), alkane-based estimates of intake were higher. Moreover, when intakes and digesta flows were related, the estimates of the proportion of digested OM apparently disappearing across the rumen (OMADR) and the efficiency of microbial protein synthesis (g N/kg OMADR) were more consistent with published estimates (see SCA 1990) when derived from alkane-based intakes (Table 2).

Although the alkane-based data in Table 2 are regarded as the more accurate (Dove *et al.* 1990), they utilise herbage intakes which were estimated from independent estimates of faecal output (dilution of infused ruthenium) and herbage digestibility (C35 alkane as an internal marker), rather than the use of dosed and natural alkanes as in the method described by Mayes *et al.* (1986) or Dove and Mayes (1991, 1996). In particular, the results depend on the assumption that the herbage C35 concentration is the C35 concentration in the consumed diet, and on the assumed faecal recovery for C35. Given that selection for plant parts can occur from within a single-species sward (Dove *et al.* 1990), both assumptions can be sources of error. Moreover, digesta flow rate measurements such as those in Table 2 require the use of cannulated animals.

As Mayes *et al.* (1995) have recently dicussed, a challenge in future grazing studies is to combine methods which can provide estimates of diet selection and herbage intake in individual grazing animals with non-invasive procedures for estimating the major products of rumen digestion, such as microbial protein. The use of the alkane-based methods can provide the necessary estimates of diet selection and intake, and there is increasing evidence that plant wax alkanes could themselves be useful digesta flow markers and that the required estimate of rumen microbial protein synthesis could be obtained using methods based on urinary markers such as total purine derivative excretion (see Mayes *et al.* (1995) for detailed discussion).

Once such techniques are perfected, areas of plant/animal interaction which are in urgent need of detailed study include the effect of differences in the shear and compression energy of fresh herbage on diet selection and intake by grazing stock (Baker and Dynes 1997), and the impact of the water-soluble carbohydrate content of herbage on diet selection (Simpson and Dove 1994) and rumen microbial protein synthesis (Dove and Milne 1994).

Table 2. Estimates of herbage intake (g OM/day) based on *in vitro* digestibilities or those derived from herbage and faecal alkanes, with corresponding estimates of the proportion of digested OM apparently disappearing across the rumen (OMADR) and the efficiency of microbial protein synthesis (g microbial N/kg OMADR)

		Stage of lactation (days)		
Measurement	Method	14	28	42
Herbage intake	*In vitro*	1776	1539	1763
	Alkane	1736	1639**	2240***
OMADR	*In vitro*	0.584	0.536	0.443
	Alkane	0.571	0.568**	0.581***
g microb. N/kg OMADR	*In vitro*	40.1	47.3	69.6
	Alkane	37.1	40.3*	44.3**

Data for 10 lactating ewes fistulated at the rumen and abomasum (Dove *et al.* 1990). For details of marker infusion and digesta sampling, see Dove *et al.* (1988). Asterisks indicate significant differences within a pair of values (* $P<0.05$; ** $P<0.01$; *** $P<0.001$ respectively).

Impact of supplementary feeding

Under Australian grazing conditions, the interaction of grazing livestock and their feed resource is often a three-way one, involving pasture, animal and supplement. Compared with the situation in which a mineral supplement is given to overcome a known or suspected mineral deficiency, supplements which are offered to make up for an inadequate quantity or quality of pasture often result in substitution between supplement and pasture. On other occasions, when there is ample herbage but it has low digestibility and protein content, supplements containing rumen-degradable protein can increase the intake of dry herbage (eg Freer *et al.* 1988). The estimation of the likely interaction between herbage and supplement thus poses a problem both for stock managers and for those attempting to represent this interaction in mathematical terms, within decision support tools (see Freer *et al.* 1997 for discussion).

The supplement intake of individual animals can be estimated using non-radioactive markers such as Cr_2O_3 (Dove and Coombe 1992), lithium chloride (Kahn *et al.* 1994) or ytterbium acetate (Curtis *et al.* 1994). There is an urgent need to combine such procedures with estimates of diet selection and herbage intake. Recent work has also extended the alkane method to the estimation of supplement intake (Dove and Oliván 1998). In this approach, the supplement is labelled with beeswax which provides it with a unique alkane 'signature', and the proportion of supplement in the total intake is estimated by treating it as one of the 'species' in the estimation of diet composition. The amount of supplement and herbage can then be calculated by apportioning the total intake (Dove and Oliván 1998). An advantage of this approach is that it is possible to estimate diet composition, supplement intake and herbage intake from the same set of chemical analyses.

ECOLOGICAL AND ENVIRONMENTAL ASPECTS OF PLANT/ANIMAL INTERACTIONS

In recent years, the alkane methods described above have been used in conjunction with other techniques, to investigate ecological aspects of the utilisation of plants by a range of wild and domestic herbivores (see discussion in Dove and Mayes 1996 and also Hulbert *et al.* 1996; Perezbarberia *et al.* 1997). Excellent examples of such applications are the investigations of diet composition and herbage intake to monitor the movement of radionuclides through grazing or browsing systems, following either the Chernobyl nuclear accident or experimental simulations of it (see Mayes 1989; Mayes *et al.* 1994; Salt *et al.* 1994; Palo and Wallin 1996).

Salt *et al.* (1994) investigated radiocaesium (^{134}Cs) ingestion by sheep from either heather (*Calluna vulgaris*) dominated vegetation or *Deschampia flexuosa* dominated grassland, following soil injection (early May) with ^{134}Cs to simulate Chernobyl fallout. Over the period between late May and July, total ^{134}Cs intake increased almost four-fold (31 to 112 kBq/day) but did not increase further by September (109 kBq/day). Over this same period, there were marked differences in the extent to which different plant species or their component parts contributed to either DM intake or to ^{134}Cs intake (Table 3). In May, the grasses as a group contributed about the same proportion of the ^{134}Cs intake as they did of the DM intake but at the later measurements, the higher ^{134}Cs concentrations in *C. vulgaris* shoots and flowers resulted in this species contributing almost twice as much of the ^{134}Cs intake as it did of the DM intake.

Table 3. Relative contributions of different plant species in heather moorland, to the intake of either dry matter (DM) or radiocaesium (^{134}Cs) by sheep

	May 1989		July 1989		September 1989	
Species/part	% of DM	% of ^{134}Cs	% of DM	% of ^{134}Cs	% of DM	% of ^{134}Cs
Dead material	17.5	6.3	19.2	3.5	9.3	2.2
Grasses[a]	74.3	81.8	21.4	9.0	10.0	3.8
Calluna pilulifera	1.6	2.0	1.6	1.0	2.4	1.3
Erica cinerea	0	0.1	3.9	0.3	0.1	0
C. vulgaris:						
Flowers	0	0	1.0	1.2	9.9	18.8
Green shoots	0.9	1.3	47.5	82.1	62.6	70.5
Dead shoots	0	0	1.1	0.9	5.0	3.1
Other[b]	5.7	8.6	4.4	2.0	0.7	0.4

Adapted from tabulated data in Salt *et al.* (1994) for sheep grazing heather moorland in north-east Scotland. [a]Grasses consisted principally of *Deschampia flexuosa, Festuca ovina* and *Agrostis* spp.. [b]'Other' consisted of *Nardus, Juncus, Luzula* and *Potentilla* spp..

In naturally-contaminated, partially-forested areas, Mayes *et al.* (1994) obtained similar results with grazing goats, in which diet composition and intake were measured using alkane-based procedures. In the plant species consumed by the goats, radiocaesium specific activity ranged from 227 (leaves of *Betula pubescens*) to 2359 Bq/kg DM (the grass *Deschampia flexuosa*). Leaves of willow (*Salix* spp.) and birch (*Betula* spp.) made up the bulk of the diet (45-90% by weight), so that the specific activity of the consumed diet was less than two-thirds of the average of the plant tissues sampled (630 v. 962 Bq/kg DM respectively). The practical significance of these results and those in Table 3 is in providing an objective basis for estimating how much radionuclide is consumed, what are the resultant levels of specific activity in animal tissues or products, and how grazing or forest management can be used to minimise these.

In even more complex plant-animal associations, such as the grazing of forest communities by moose (Palo and Wallin 1996), the increased extent of diet choice both within and across seasons, coupled with differences between plant species in radionuclide uptake, have required the use of simulation modelling to investigate likely trends in the cycling of radionuclides (Palo and Wallin 1996). For example, studies with moose (*Alces alces*), an economically-important game animal, have indicated that the variability in tissue ^{137}Cs levels between individual animals and years is due substantially to a corresponding variability in diet composition (Palo and Wallin 1996).

NUTRIENT CYCLING IN GRAZED PASTURES

In grazing systems, animals usually select diets which differ in botanical and chemical composition from the herbage on offer. In addition, and as White *et al.* (1997) recently put it "...the mobility of animals in the system and the pattern of return of excreta have an important influence on the cycle of nutrients". Two nutrients of particular concern in Australian grazing systems are nitrogen (N) and phosphorus (P). The former ultimately provides the protein required by grazing animals and much of the grain protein in ley-farming systems, but it is also a possible contributor to soil acidification through nitrate leaching. Phosphorus, in the form of superphosphate application for improved plant and animal production, represents the major discretionary expenditure on fertiliser by Australian graziers.

Increasingly in temperate Australia, there is a need for management systems which minimise the effects of nitrate on soil acidity and which optimise the cost-effectiveness of fertiliser application. Computer models of nutrient cycling under grazing offer an ideal way of testing new management options, but until recently the techniques available for estimating diet composition and herbage intake by animals were not accurate enough to allow estimates of nutrient inputs from different sward components. Moreover, urinary nutrient returns were difficult to estimate in the absence of reliable and non-invasive techniques to estimate urine output.

Dove and Simpson (1997a) using alkane-based procedures estimated herbage intake and the botanical composition of the diet in sheep grazing in south-east Australia. This allowed, in individual animals, the estimation of N intake from individual plant species and thus total N intake, while faecal N excretion was calculated from the estimated faecal output and its N content. Predictions of N intake, faecal N excretion and urinary N excretion were obtained using the pasture and animal data as inputs to the decision support package GrazFeed (Freer *et al.* 1997). Estimated and predicted N intakes agreed well (25.3±1.20 v. 26.2±1.69 g N/day, respectively), and predicted urinary N excretion was closely related to predicted and thus also to estimated N intake. In winter and spring, the predicted urinary N excretion amounted to 73.1% of estimated N intake and 75.5% of the total N excretion, values similar to those in previous reports (see White *et al.* 1997). These data are being studied further, to evaluate the effects of the liming of pastures, and the effects of annual versus perennial pastures, on the transfer of N to nitrate in ground water, with possible effects on the rate of soil acidification.

From a knowledge of the the P content of the individual plant species consumed and the P content of faeces, similar estimates of P transactions can be made. Dove and Simpson (1997b) recently estimated P intakes and faecal P excretions in sheep grazing the same pastures in winter, spring and summer (Table 4). The P content of the consumed diet was similar in winter and spring, but markedly lower in the dry summer herbage. Mean herbage P intakes were also similar in winter and spring (Table 4) and ranged from 2.5-8 g/d compared with a range of 0.5-4 g/d in summer. There was a positive, linear relationship between P excretion in faeces and P intake, but upon closer examination, the relationships between faecal P excretion and P intake differed between the winter/spring (green herbage) and summer (dry herbage). These results suggest that from the point of view of the modelling of P kinetics under grazing, it is not possible to assume a single, simple

Table 4. Mean values (±s.e.) for the phosphorus (P) content of the consumed diet, P intake and faecal P excretion in sheep grazing improved pastures in south-eastern New South Wales

	Winter	Spring	Summer
Diet P content (% OM)	0.52±0.031	0.47±0.018	0.20±0.017
P intake (g/day)	4.7±0.33	4.5±0.22	1.7±0.19
Faecal P excretion (g/day)	3.9±0.17	3.5±0.11	1.6±0.08

Derived from data in Dove and Simpson (1997b).

relationship between P intake and faecal P excretion. They also emphasise the need to obtain estimates of urinary P excretion which, while not the major route of P excretion, will occur in grazing animals in positive P balance (SCA 1990).

In principle, a similar approach could be used to monitor the cycling of inorganic and organic forms of P, and of other key minerals such as sulphur, calcium, magnesium, potassium, copper, molybdenum, zinc or selenium. This would overcome the problem already referred to above and by Underwood (1966) that "...Selective grazing could ... greatly influence actual mineral intakes by animals".

EMERGING OPPORTUNITIES IN THE STUDY OF PLANT/ANIMAL INTERACTIONS

Is herbage water-soluble carbohydrate important in diet selection/intake?

Twenty-five years ago, Michell (1973) presented data for penned sheep offered a range of pasture species, indicating that the animals consumed more of a given species when it contained higher concentrations of water-soluble carbohydrate (WSC). In the case of perennial ryegrass, this was so even when the overall digestibility remained the same. More recently, Simpson *et al.* (1993) and Simpson and Dove (1994) reported that manipulation of WSC in senescing annual grass pasture resulted in higher intakes when WSC was increased. Moreover, the preferences exerted by both penned and grazing sheep for different plant parts were closely related to the WSC in that part (see Simpson *et al*. 1993).

The existence of a preference for herbage of high WSC content is important not just in relation to likely increases in intake, but also because the higher rumen propionate concentrations arising from higher herbage WSC content can lead to increased rumen microbial protein production (see SCA 1990; Dove and Milne 1994). For example, Dove and Milne (1994) found a linear relationship between rumen propionate concentration and the abomasal flow of non-ammonia nitrogen (NAN) in ewes grazing perennial ryegrass pastures (Figure 2) of similar digestibilities.

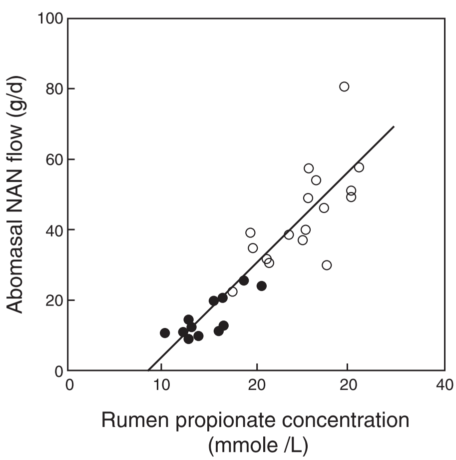

Figure 2. Influence of rumen propionate concentration (mmol/L) on the abomasal flow of non-ammonia nitrogen flow (g NAN/day) in ewes grazing perennial ryegrass pastures in (the British) late spring/summer (open symbols) or autumn (closed symbols). Adapted from Dove and Milne (1994) with the kind permission of the *Australian Journal of Agricultural Research*.

Hence an important aspect of the 'plant/animal interface' requiring further examination is the quatitative significance of increased WSC content of pastures, in relation both to preference and to total intake. In our studies with senescing annual ryegrass pastures, preferences for high-WSC plant fractions were made quickly and were repeatable (see Simpson and Dove 1994). Similarly, Ciavarella *et al.* (1998) in the present Conference, have reported on the use of a pasture-shading technique to generate differences in herbage WSC content under field conditions, coupled with an alkane-spraying technique to establish preference. Their results indicate that over a single day of grazing, sheep given a free choice between shaded (low WSC) and unshaded (high WSC) phalaris pasture did not distribute their grazing preference equally across the two areas, but were 2.8 times more likely to consume the high WSC material. The above results, plus recent data for grazing cattle (Mayland *et al.* 1997; Shewmaker *et al.* 1997) indicate that taste and/or olfactory cues are operating in the process of diet selection, and are operating quickly and repeatably. In turn, this suggests that useful areas for future study would be in the confirmation of preferences for high levels of WSC in herbage and its exploitation through plant breeding, and in the identification of diet selection cues and the possible exploitation of these in pasture management, as foliar sprays to increase the utilisation of otherwise non-preferred herbage.

Biomechanical features of herbage and the concept of 'forage consumption constraint'

R.H. Weston proposed the term 'forage consumption constraint' (FCC), to quantify the difference between the actual feed intake of an animal and the amount it would need to consume to satisfy its capacity to use energy, in the absence of any constraints (see Weston 1996 and Baker and Dynes 1997 for recent discussion). This has proved a useful concept, to the extent that the fibre fractions of herbage are more closely related to FCC than they are to voluntary feed intake (see Weston 1996). In particular, Baker and Dynes (1997) have recently discussed the strong positive correlations between the energies required to shear (Henry *et al.* 1996) and to comminute herbage material and the magnitude of the FCC, when no other factors constrain intake. Clearly, factors other than the digestibility of herbage frequently constrain intake (*ie* increase FCC) and Baker and Dynes (1997) cite recalculations from a range of published studies indicating the extent to which a given FCC was reduced by making good intake limitations related to forage tannin or mineral concentrations (see their Table 2).

As has been discussed recently (Dove 1996a,b; Baker and Dynes 1997), the relevance and application of the concept of FCC under field conditions depends upon having accurate estimates of the characteristics of the consumed diet, the intake of that diet and the capacity of the grazing animal to use energy. The approaches to identifying, in individual animals, the composition of the consumed diet and the amount eaten have been described above. These methods ultimately need to be combined with telemetric methods to estimate chewing and rumination activities under field conditions, in order to obtain the information on the biomechanical characteristics of the herbage (shear and comminution energies; eg Klein *et al.* 1994).

FUTURE RESPONSIBILITIES

The techniques and results described in this Lecture, combined with earlier studies conducted both in penned animals and in the field, place us in a better position than ever before to extend to the field situation, the information obtained in indoor studies. Results obtained in indoor work will continue to be valuable in our understanding of the interactions between grazing animals and their pasture resource, but ultimately, similar measurements need to be made under grazing conditions since, as a recent publication so succinctly put it (Corbett and Ellis 1997);

'The sward is mightier than the pen'

Although this Lecture contains many references to the need to characterise the consumed diet, understanding will only come from the integration of three sources of information: the requirements of the animal; the characteristics of the consumed diet as they relate to those requirements; and the characteristics of the sward as they influence the nature of the consumed diet. As animal scientists, we have been highly successful in studying and quantifying the first, due in no small measure to the efforts of colleagues such as Underwood. We are also having increasing success in quantifying the nature of the consumed diet. We need to continue our efforts in both these areas but if our increased understanding is to be translated into increased profits in animal production, our results will have to be related to the nature of the pasture, since this is what graziers have to manage. More effort needs to be directed towards the quantification of the physical and chemical composition of the herbage on offer and especially the way in which that herbage is presented to the animal.

A further responsibility remains. In the Introduction to this Lecture, I quoted Underwood's words of almost 70 years ago, that "...economic prosperity depends...on the productivity of flocks and herds...", words which were in fact used in the justification of the study of pastures and their nutritive value. A decade ago, a previous Underwood Lecturer (McDonald 1988) reminded us that this productivity depends greatly on the interaction of animals with their pasture and the pasture with its underlying soil. He quoted the following words written in 1931 by Sir Charles Martin, an Underwood contemporary and second Chief of the CSIR Division of Animal Nutrition:

"In attacking practical problems in sheep...production, it is just as essential to obtain accurate information regarding pastures as it is to accumulate data regarding the feeding and metabolism of sheep...Success can be expected only when the agrostologist, the soil chemist and the [animal] physiologist collaborate."

It is to be hoped that in the future, research funds continue to be made available to support such collaborations.

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