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in

Gordon I.J. (ed.), Rubino R. (ed.).
Grazing behaviour of goats and sheep

Zaragoza : CIHEAM
Cahiers Options Méditerranéennes; n. 5

1994
pages 13-28

Animal-based measurement techniques for grazing ecology research: a review

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SUMMARY - Grazing ecologists have available to them a suite of research techniques to measure aspects of plant/animal interactions. This review focuses on animal-based techniques and describes the methods available to tackle questions concerned with the intake, foraging behaviour, diet composition and location of free-ranging large mammalian herbivores.

Key words: Grazing ecology, techniques, intake, diet composition, grazing behaviour, location.

RESUME - "Révision de techniques de mesure basées sur l'animal pour la recherche en matière d'écologie de pâturage". Les écologues en matière de pâturages disposent d'une série de techniques pour mesurer les aspects des interactions plante/animal. Cette étude traite des techniques basées sur l'animal et décrit les méthodes disponibles pour étudier les aspects relatifs à l'ingestion, le comportement alimentaire lié aux fourrages, la composition du régime et la localisation des grands mammifères herbivores dans les parcours.

***Mots-clés** : Ecologie du pâturage, techniques, ingestion, composition du régime, comportement de pâturage, localisation.*

Introduction

Grazing ruminants form the backbone of most of the world's ruminant livestock enterprises (Fitzhugh *et al.*, 1978), particularly in marginal areas where cereal crops are of low productive potential. These animals graze a variety of vegetation types from simple sown monocultures, typical of intensively managed grassland, to complex mixtures of vegetation communities, typical of rangelands. The level of production obtained from animals grazing these vegetation types is dependent upon their ability to obtain a diet adequate to meet their nutrient requirements for maintenance, growth and reproduction. This in turn is regulated by a series of short-term tactical decisions made by the animal about, for example, diet selection and how long to search between bites. These decisions influence the rate of food intake and nutritional content of the diet. In the longer term, strategic decisions concern the length of time to spend feeding and where to feed, given topographic influences on energy expenditure and distance travelled between foraging sites, water and shelter (Fig. 1). This suite of decision-making processes is defined as the foraging strategy of the animal. If we are to make the most efficient use of the plant and animal resources available in marginal areas it is essential to improve our understanding of the foraging strategies of the herbivores which use these ecosystems.

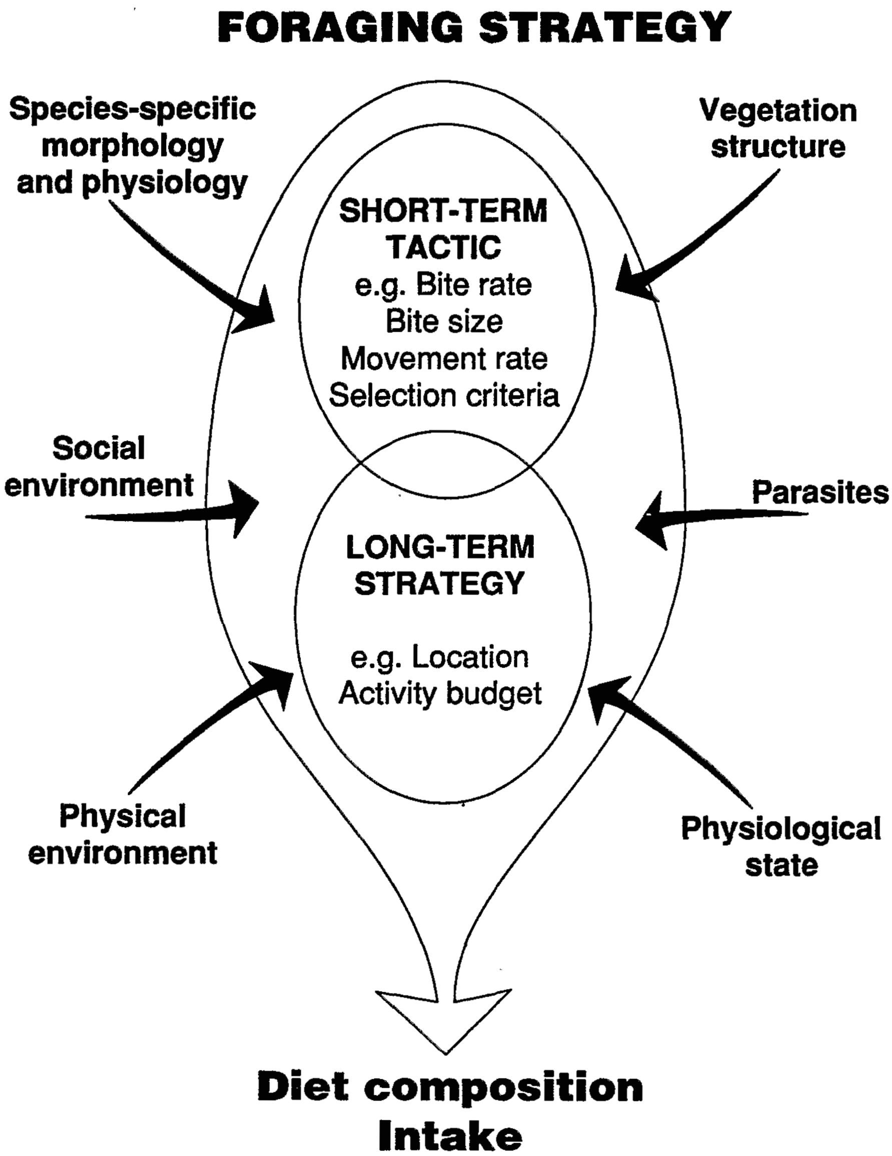

Fig. 1. Schematic presentation of interactions between the tactical and strategic components of foraging strategy and external factors.

To date, most studies of the foraging strategy of ruminants have been descriptive catalogues of their diets at the taxonomic or plant part level and of their daily intake (e.g. Van Dyne *et al.*, 1980). The information is of limited predictive value outside the circumstances and site from which they were obtained and do not advance our general understanding of foraging strategy and diet selection. Through an understanding of the mechanisms involved in the decision-making processes of the foraging animal it will be possible to develop more widely applicable predictive models to meet agricultural, conservation or amenity objectives. In order to develop this understanding researchers require a range of techniques to interpret both short-term tactical and long-term strategic foraging strategy decisions.

This review describes recent research on the development of techniques for measuring the foraging behaviour of ruminants. The review will focus on technique development in four areas of measurement: intake rate (both short- and long-term), foraging behaviour (e.g. bite rate, feeding time, mastication rate, movement rate), diet composition and location of the animal (Fig. 2).

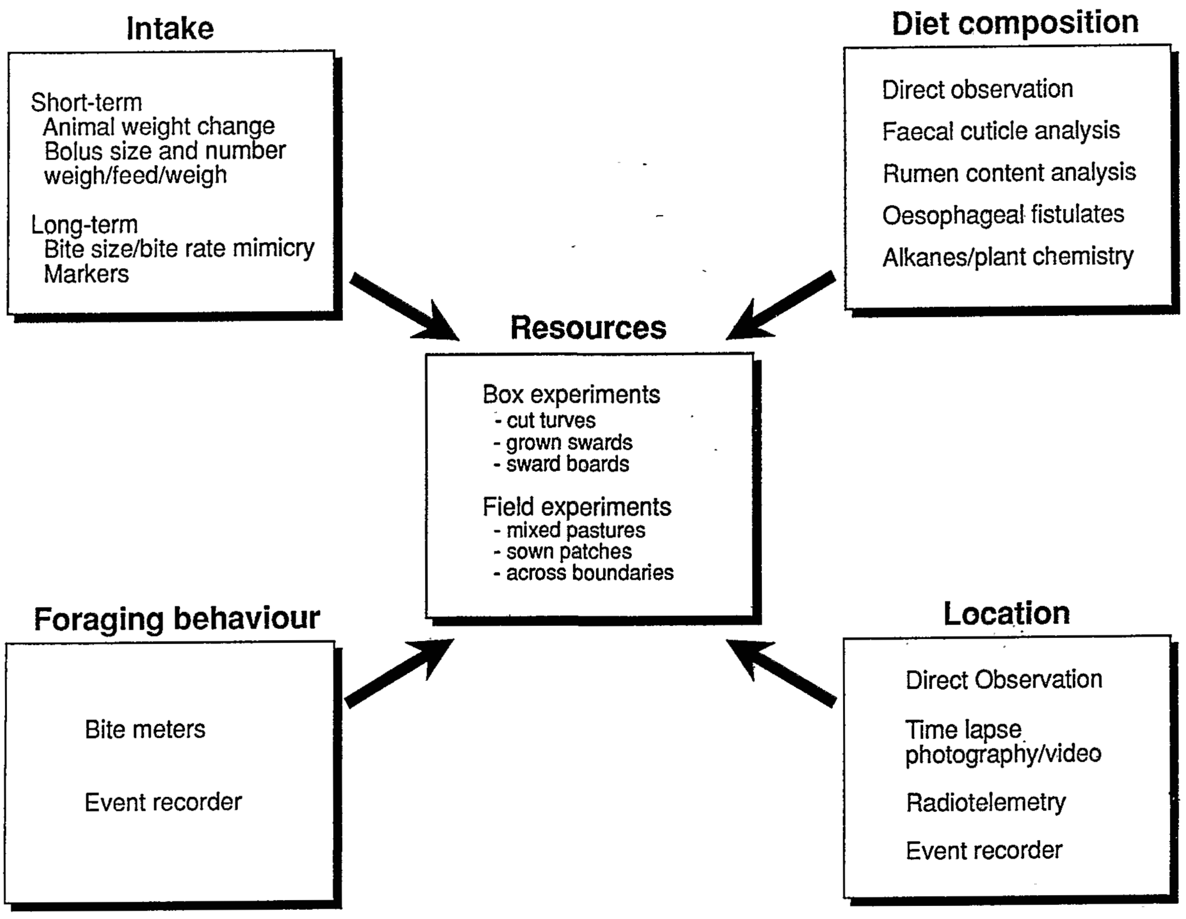

Fig. 2. Approaches and techniques used to measure the various components of the foraging strategy of domestic livestock.

Intake rate

The principal reasons for measuring herbage intake are (1) to understand the relationship between sward structure and herbage intake, (2) to explain between animal variation in intake and performance and (3) to explain variation in animal performance associated with different grazing regimes and management practices. All of the techniques used to measure herbage intake must meet the criteria of causing minimal disturbance to the animal, having little impact on its welfare, having a precision suitable for the purposes of the measurement and giving unbiased results. In some circumstances, it is important to have low labour inputs in order to minimize costs.

While foraging an animal takes a series of bites of varying size from the herbage on offer. The combination of the bite size and the short term rate of biting is defined as the instantaneous intake rate, with units given in mg s^{-1} or g min^{-1}. Over the day the animal spends a certain amount of time grazing and the intake during this time period is defined as the long-term intake rate, in kg d^{-1} (Fig. 3).

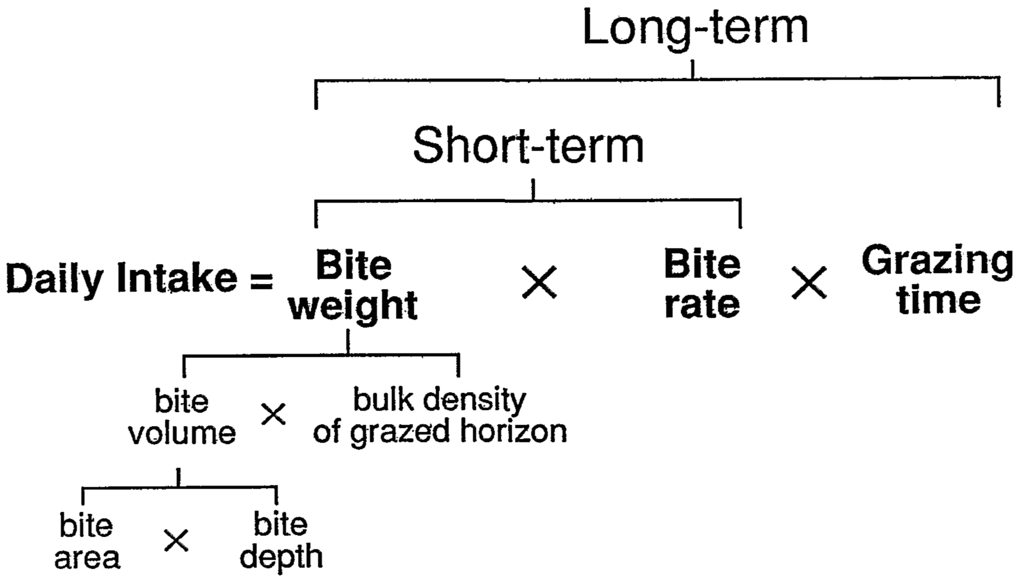

Fig. 3. Components of daily herbage intake.

Short-Term

Two separate approaches have been used to estimate the short term intake of the grazing animal. The first allows the animal to range freely across a pasture and exhibit its normal foraging behaviour, the second relies upon confining the animal to a pen or arena and providing it with plant material to consume.

Four techniques have been developed for estimating the intake rate of free-ranging animals. In the first an observer mimics the bite size by visual observation of bite and hand plucking similar vegetation and measures the bite rate of a tame free-ranging animal (Bjugstad *et al.*, 1970; Bryant *et al.*, 1980). The disadvantages of this technique are that it is time consuming, it is difficult to follow an animal at night and it is unreliable due to, for example, inter-observer differences in estimation of bite size. Secondly, short-term changes in live weight before and after free-range grazing, measured using very accurate balances, can be used to estimate short-term intake rate (Penning and Hooper, 1985). It is necessary to correct live weight changes for faecal, urinary, respiratory and other obligatory live weight losses. The accuracy of this technique is proportional to the length of time over which the intake is being integrated. The third technique uses the fact that there is a strong correlation between the number of boluses swallowed by an animal while feeding and its intake of herbage (Forwood and Hulse, 1989). A number of techniques have been developed to determine the number of food boluses swallowed and the rate of swallowing of the free-ranging animal (Stuth *et al.*, 1981; Forwood *et al.*, 1985). Theoretically, this allows intake rate to be measured instantaneously. However, because of differences between individual animals in the weight of the bolus (in relation to the animal's live weight and the type of forage consumed), calibration equations are required for each circumstance in order to estimate intake (Forwood *et al.*, 1991). The method also involves surgical implants into animals to record the number of boluses swallowed and potential associated welfare problems. Finally, short term intake rate and bite size can be estimated from animals prepared with oesophageal fistulas through the collection and weighing of extrusa over a know time period and the simultaneous recording of bite rate (Stobbs, 1973). This technique suffers similar methodological problems to those described for the bolus measurement technique. Furthermore, it provides unreliable estimates because of incomplete extrusa recovery, the extent of which varies with the individual (R.H. Armstrong, pers. comm.), and the use of foam sponges to increase the recovery can affect the normal grazing behaviour of the animal (I.J. Gordon, pers. obs.).

In order to have more control over the plant material on offer to the grazing animals a number of methods have been developed which incorporate the presentation of plant material to animals confined within pens or arenas. The plant material may be presented in the form of turves cut from representative areas of plant material (Mursan *et al.*, 1989), in trays managed in order to provide plant material of a given sward characteristic (Illius *et al.*, 1992) or plant material anchored to a board (Black and Kenny, 1984; Spalinger *et al.*, 1988). Using an alternative approach, Burlison *et al.* (1991) used a 'grazing cage' to confine animals onto very small areas (2500 cm^2) of pasture. These techniques allow plant variables to be controlled very precisely and estimates to be made of the short-term intake rate (usually less than 5 minutes) and its components. These small scale trials have several advantages over larger scale approaches because they allow observers to make detailed and in some cases automated measurements of sward characteristics, bite depth, bite weight, bite rate and diet selection. Direct estimates of bite area and volume can also be obtained, allowing the complete set of bite variables to be related to the characteristics of the vegetation grazed (Fig. 3). However, by confining animals their normal foraging behaviour may be altered. As yet no critical test of the validity of this approach has been applied although, in general, the results obtained using these techniques agree well with published values obtained from free-ranging animals (Mursan *et al.*, 1989).

Long-term

A number of methods have been developed for measuring long-term (daily) intake rate (see reviews of Leaver, 1982 and Dove and Mayes, 1991). The majority of the pasture-based methods of intake estimation (Meijs *et al.*, 1982) are of limited value except on simple swards because of the errors associated with the measurement of pasture growth and senescence (Grant, in press), the difficulty of estimating intake from vegetation community mosaics and their inability to provide estimates of between-animal variation in intake. A more direct approach to measuring intake using animal-based methods is frequently used (Corbett, 1981; Mayes, 1989). Animal-based methods of estimating intake (I) have in the past relied on the measurement of faecal output (F) and diet digestibility (D) (Van Dyne, 1969; Kotb and Luckey, 1972) and estimating intake as:

$$I = \frac{F}{(1\text{-}D)}$$

Total collection methods for estimating faecal output are laborious and possibly affect the normal grazing behaviour of the animals involved (Armstrong and Eadie, 1977). Faeces output is usually estimated, therefore, from the concentration of an orally dosed indigestible marker (e.g. Cr_2O_3, C_{36}n-alkane) in the faeces (Corbett, 1981; Mayes, 1989; Dove and Mayes, 1991). The faecal output is estimated from the concentrations of these indigestible markers in the faeces (Mf) and the daily dose of marker (Mh) administered:

$$F = \frac{(Mh \times R^*)}{Mf}$$

*the recovery of the marker in the faeces is assumed to be 1.00 for Cr_2O_3 and 0.98 for C_{36} n-alkane.

The Tilly and Terry (1963) method for estimating the 48-h *in vitro* digestibility of extrusa samples from oesophageal fistulates or hand plucked samples is the most frequently used method of determining the digestibility of the diet consumed (Van Dyne, 1969). This method assumes that the fistulates consume a diet similar to that of the animals for which faecal output has been measured and that the *in vitro* estimates of digestibility reflect *in vivo* digestibility. Both of these assumptions appear not to hold in all cases (Holechek *et al.*, 1986; Coates *et al.*, 1987). A less intrusive technique to predict digestibility is to use faecal concentrations of N which are correlated with forage digestibility (Greenhalgh and Corbett, 1960). Although they have been used extensively on simple pastures these faecal indices require calibration for different sward types, species of animal and animals of different physiological state and are of little value where the animal might consume a diet containing protein precipitating plant metabolites (Hobbs, 1987). A preferred technique would be to use internal indigestible markers (e.g. lignin, silica) to estimate *in vivo* digestibility (D) directly using the concentration of the component in the diet (Cd) and faeces (Cf) from the equation:

$$D = 1 - \frac{Cd}{Cf}$$

These marker techniques, however, have not proved reliable. Recently, Mayes *et al.* (1986) have shown that n-alkanes found in the cuticles of plants can be used as both internal and external markers to estimate diet digestibility and intake in sheep, goats, cattle and red deer.

Currently, there is research being conducted on the use of slow release markers from spring-loaded capsules (Mayes *et al.*, 1991). These devices remain in the rumen and deliver a constant doze of marker over a period of up to 30 days increasing the accuracy of intake estimation. They also bring closer the possibility of estimating the intake and digestibility of wildlife species which can only be handled very infrequently.

Foraging behaviour

Free-ranging ruminants respond to the quantity and distribution of vegetation on offer by altering their foraging behaviour. For example, the rate of intake by sheep on homogeneous ryegrass (*Lolium perenne*) pastures increases in proportion to the herbage mass or height on offer (Hodgson, 1977; Penning, 1986; Penning *et al.*, 1991). In an attempt to maintain intake, sheep respond to a low sward height by taking more bites per minute and grazing for longer (Fig. 4). However, below about 6 cm these behavioural mechanisms are unable to compensate for changes in bite size; as a result the intake rate drops.

The primary foraging behaviour variables which researchers are interested in are bite rate (prehension, harvesting), mastication rate, feeding time and movement rate. A number of mechanical and electronic devices have been developed to measure one or more of these variables (Stobbs, 1970; Anderson and Kothmann, 1977; Penning, 1983; Matsui and Okubo, 1989). All of these systems monitor jaw movements, either digitally or in analogue form. In order to determine whether the animal is grazing or ruminating, the inter-bite interval or the shape of the waveform is analyzed (Fig. 5). The more sophisticated devices (e.g. Penning, 1983) allow a number of behavioural parameters to be derived from the recordings (Table 1). The majority of the jaw movement monitoring devices are carried on the animal and requiring the animal to be handled regularly in order to retrieve the data. A more flexible system involves the data being transmitted to a remote receiver via radio telemetry (Nichols, 1966). The 'bite-meter' system of Penning (1983) is currently being modified in order to transmit and record the jaw movement information remotely. This should reduce the frequency of animal handling to once every 4 to 5 days (T. Phillips, pers. comm.).

An alternative approach is to use a manually operated computer based program to capture foraging data (Owen-Smith, 1979; Demment and Greenwood, 1987; Unwin and Martin, 1987). This can be extremely time consuming and unless a video-recording is made the observer can only sample a limited number of individuals at one time. In addition it relies on the animals being easily observable. The presence of a human observer can also alter the behaviour of even tame animals (Owen-Smith and Cooper, 1987). However, unlike the automated techniques described above this technique does allow the gathering of other contextual data, such as the distance to a dominant or subordinate animal and the slope and aspect of the feeding station.

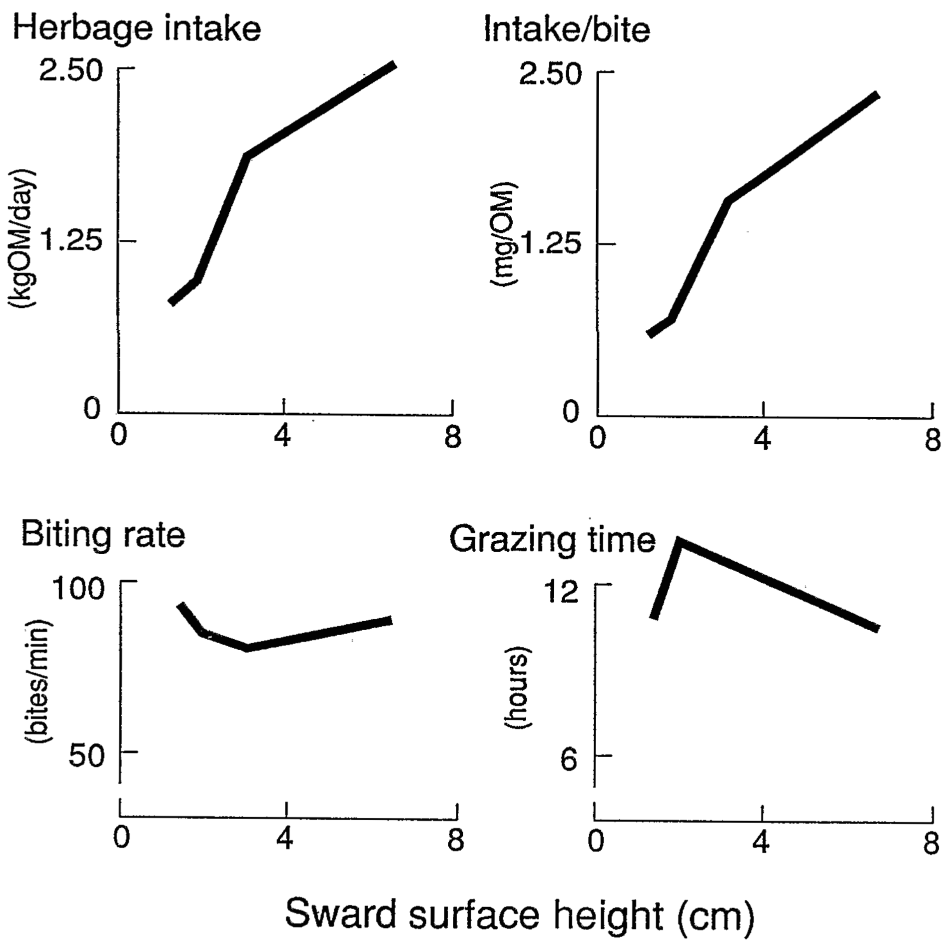

Fig. 4. The influence of sward height on the ingestive behaviour and herbage intake of ewes under continuous stocking management. After Bircham (1980).

Diet composition

A number of techniques have been developed for assessing the diet composition of the free-ranging animal (McInnis *et al.*, 1983). These techniques range from simply following an animal and obtaining hand-plucking samples which mimic each bite taken (e.g. Bryant *et al.*, 1981) to the use of a marker unique to each species or plant form in the diet and identified in the faeces (Mayes, 1989; Dove and Mayes, 1991). Each technique has its advantages and disadvantages; for example, the hand plucking technique requires tractable animals which can be approached closely enough to facilitate observation and is of limited use where plants occur in intimate mixtures. On the other hand, the marker technique requires expensive analytical equipment to measure marker concentrations in the food and faeces and is limited at present to a small number of plant species.

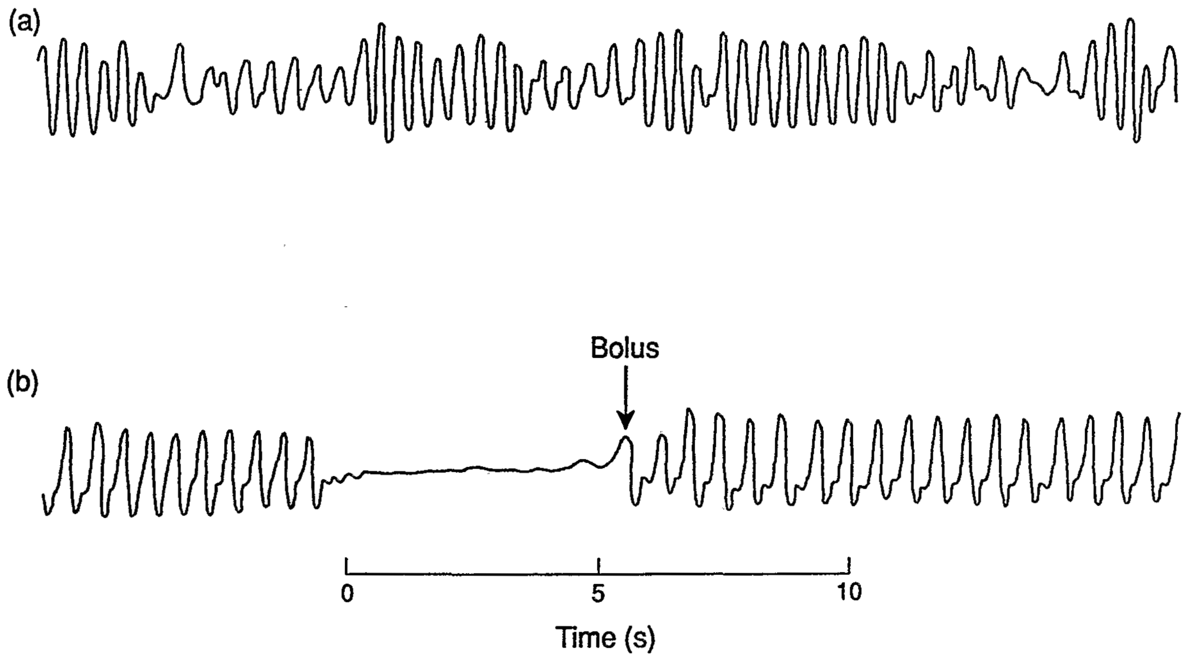

Fig. 5. Oscilloscope traces of the output from a noseband recording jaw movements in a sheep during a) grazing and b) rumination bouts. After Penning (1983).

For studies on wildlife species plant cuticular material in the faeces is compared with reference collections from known plant species to estimate diet composition (Crocker, 1959). However, because of differential digestion of plant species within the rumen (Rice, 1970; Slater and Jones, 1971) and the typically high proportion of unidentified cuticular remains in the faeces (McInnes *et al.*, 1983) this technique is of little value.

The use of oesophageal fistulation has been relatively successful in determining the diets of domesticated animals (Vavra *et al.*, 1978). It has not been extensively used in wild herbivores. The problems with this technique are:

i. Requirement for surgery (Rice, 1970).

ii. The short time period for collection of samples and the small area over which the samples are collected which may lead to biases (Lesperance *et al.*, 1974; Coates *et al.*, 1987).

iii. That the grazing behaviour of fistulated animals may differ from that of intact animals (Engels and Malan, 1973; but see Forbes and Beattie, 1987).

Table 1. A portion of typical results file from a recording of the jaw movements of grazing sheep (programme produced by Penning pers. comm.)

406 Eating Minutes (29%) of the Day
153.9 (SD 15.8) Jaw Movements per Minute
40.3 (SD 13.2) Prehension Bites per Minute
113.6 (SD 17.4) Mastication Bites per Minute
Mean of 2.8 Mastication Bites per Prehension Bite
441 Ruminating Minutes (32.5%) of the Day
98.3 (SD 29.5) Ruminating Chews per Minute
78.7 (SD 14.4) Chews per Bolus
1.1 Boluses per Minute
512 Idling Minutes (37.7%) of the Day

Overall the results from oesophageal fistula extrusa provide as yet the most accurate method for determining diet composition as long as the fistulated animals are accustomed to the vegetation community before the sample is gathered (McInnis *et al.*, 1983).

Unique plant markers are increasingly being used to estimate diet composition. For example, differences in the calcium content and ^{13}C:^{12}C ratio of legumes and grasses have been used to estimate their proportion in the diet (Playne *et al.*, 1978; Jones *et al.*, 1979). However, these markers are limited in their use. For example, in the temperate regions C_3 plants are rare. More recently, the differences in the odd-chain n-alkane (C_{25}-C_{35}) profiles between plants has been used as a tool to estimate diet composition (Mayes, 1989; Dove and Mayes, 1991). These preliminary investigations have shown the effectiveness of using this technique for quantifying diet composition for small numbers of species.

Location

Even in relatively homogeneous plots, animals distribute themselves and conduct their behaviour unevenly (Arnold, 1984/5). In more complex ecosystems, such as rangelands, the spatial dispersion of the resources will affect the location of the animals. The decision making processes invoked by the foraging animal may differ in relation to the landform scale (Senft *et al.*, 1987). By recording the location of animals, researchers are able to answer questions about the distribution of impact of livestock on the vegetation and the effect of topographic features on the relative use of resources.

At its most simple this type of information can be gathered by direct observation (Attwood and Hunter, 1957; Arnold, 1984/5), with the animals being located either at exact points or within grid squares on a map. However, this is time consuming and requires specialized night-vision equipment if information on nocturnal distribution is to be gathered (Boag *et al.*, 1990). Systems using video cameras and computer aided image analysis or radio-telemetry (Kenward, 1987) are less time consuming and are likely to provide the required information more efficiently. Computer technology can be used to manually or automatically digitise the information in a format which facilitates analyses. These systems are still in their infancy but are likely to develop rapidly in the near future.

Conclusions

There is an increasing awareness of the importance of understanding the foraging strategy of domestic livestock in the development of efficient management systems to meet agricultural and environmental goals. Grazing ecologists now have a suite of techniques available to measure the components of the foraging strategy of free-ranging livestock. Many of these techniques have been developed and tested for agricultural species grazing simple monocultures. As researchers increase the complexity of the questions they are asking and move on to understand the foraging strategy of herbivores grazing complex mixtures of plant communities, new techniques will have to be developed to meet the requirements. Technique development is, therefore, likely to remain a fruitful area of research into the future.

Acknowledgements

Thanks go to J.A. Milne for commenting on previous drafts of the manuscript. W. Sherrifs kindly drew the figures.

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