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Dietary Selection by Domestic Grazing Ruminants in Temperate Pastures: Current State of Knowledge, Methodologies, and Future Direction

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Abstract

Ruminants grazing mixed-species pastures face many choices, including when and where to graze and how much herbage to consume. These choices affect not only the nutritional status of the animal, but also sward composition and nutritive value through selective defoliation. Limited research has been conducted in the area of dietary selection and preference, most of which has been limited to simple model systems often involving a choice between only two herbage species. Although these studies have provided a vital tool to allow understanding of the fundamental principles of foraging behavior, in reality, grazing ruminants are faced with more complex situations. Understanding and managing animal preferences in mixed swards and thereby altering dietary selection can result in greater primary (plant) and secondary (animal) productivity. Key issues to improve this understanding include a better linking of behavioral and nutritional studies, a better understanding of the genetic factors influencing diet selection, and the development of more explicit spatial models of foraging behavior that incorporate multiple scales of decision making. This article, as part of a set of synthesis articles, reviews the current state of knowledge and research methodologies related to diet selection of grazing domestic ruminants with particular reference to improved temperate grazing environments, including how well we understand each part of the complex decision-making process a grazing ruminant faces, the links with primary and secondary productivity, and developments in methodologies. Finally, we identify key areas where knowledge is lacking and further research is urgently required.

Resumen

Los rumiantes en condiciones de libre pastoreo tienen diferentes opciones, incluyendo cuando y donde pastorear y cuanto forraje consumir. Estas opciones afectan no sólo el estado nutricional del animal, sino también la composición y valor nutritivo de las especies a través de pastoreo selectivo. La investigación en el área de selección de dieta y preferencia es escasa, y principalmente se limita a un modelo simple de dos especies Estos estudios han proporcionado una herramienta vital para entender los principios fundamentales del comportamiento del pastoreo, en realidad los rumiantes en pastoreo enfrentan situaciones más complejas. Comprender y manejar la preferencia del animal en potreros mixtos, y manipular la selección de la dieta puede resultar en una mayor producción primaria (planta) y secundaria (animal). Algunos elementos claves que ayuden a conocer este proceso son una mejor relación entre estudios de comportamiento y nutricionales, un mayor entendimiento de los factores genéticos que afectan la selección de la dieta, y el desarrollo de modelos espaciales de comportamiento en pastoreo incorporando diferentes escalas en la toma de decisiones. El presente trabajo, como parte de un conjunto de manuscritos, revisa el nivel de conocimiento así como la metodología relacionados con la selección de la dieta por rumiantes en pastoreo con particular referencia a pasturas mejoradas en ambientes templados, incluyendo partes del proceso de toma de decisiones que el rumiante en pastoreo enfrenta, las conexiones entre productividad primaria y secundaria y el desarrollo de metodologías. Finalmente, se identificaron las áreas claves en donde el conocimiento es limitado y se requiere más investigación.

Key Words: diet selection, grazing behavior, methodologies, ruminants

INTRODUCTION

Pasture-based systems for domestic ruminants in temperate regions are currently undergoing a revival of interest based on a number of true and perceived benefits. Grazed herbage is the cheapest food resource for domestic ruminants. Grazing reduces the high inputs of labor, equipment, and fossil fuels associated with confinement feeding of harvested forages and therefore can make a significant contribution to the sustainability of animal agriculture and thus rural communities (Parker et al. 1993; Kriegl and McNair 2005). Further, there has been increased consumer interest in food production methods and in the potential nutritional benefits of pasture-raised animal products (Clancy 2006; Sooby et al. 2007).

Despite the potential advantages of pasture-based systems, there are limitations, including limited herbage availability and accessibility (McGilloway and Mayne 1996; Kolver and Muller 1998; Realini et al. 1999), limited energy intake (Kolver and Muller 1998); and low daily herbage dry matter intake (DMI), which has been implicated as a major factor limiting primary

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(plant) productivity and impacting secondary (animal) productivity of pasture-based livestock production systems (Leaver 1985; Kitessa and Nicol 2001; Animut et al. 2005). Control of herbage DMI in grazing domestic ruminants is exceedingly complex and has been extensively reviewed (Forbes 1995, 1996; Weston 1996; Fisher 2002). Many factors are involved in determining herbage DMI, including 1) energy demand of the animal (Weston 1996; Hodgson and Brookes 1999; Fryxell 2006), 2) physical satiety factors associated with ruminal fill or distention of the gastrointestinal tract (Forbes 1996; Hodgson and Brookes 1999; Fisher 2002), 3) feeding motivation (Hodgson and Brookes 1999), and 4) the availability and accessibility of herbage (Penning et al. 1991; Hodgson and Brookes 1999; Drescher 2003). Herbage DMI is therefore the result of a dynamic combination of animal, rumen, and plant factors (negative or positive stimuli).

Despite considerable literature on gross herbage DMI, there has been less emphasis on the role of dietary selection. A grazing ruminant is confronted with a complex food source that is heterogeneous in both spatial and temporal dimensions, and contains many different plant species. For the sake of definition, preference is what the animal chooses to eat in an unrestricted environment, and selection is defined as preference modified by environmental circumstances (Hodgson 1979). Within the constraints imposed by the environment and by its own anatomy and internal state, the animal must make behavioral choices, including placement of individual bites, choice of grazing area, specific plant species/parts to consume, or time of day to concentrate the foraging activity. These choices will not only affect the nutritional status of the animal, but will also feed back on the productive capacity of the sward due to the resulting pattern of defoliation. An understanding of the fundamental processes of selective grazing behavior is a prerequisite for the design of efficient grazing management systems.

A set of synthesis articles was developed that provides a comprehensive overview of diet selection of grazing ruminants. In this article we provide a summary of the current state of knowledge and research methodologies regarding dietary selection on pasture. Discussion includes how well each part of the complex decision-making process a grazing ruminant faces is understood, the links with primary and secondary productivity, and developments in methodologies. Finally we identify key areas where knowledge is lacking and further research is urgently required.

THE DYNAMICS OF DIETARY SELECTION

Grazing sheep and cattle prefer a mixed diet (Rutter et al. 1997c; Prache et al. 2000; Villalba et al. 2004), showing partial preferences for certain functional groups of plants such as legumes (Parsons et al. 1994; Hester et al. 1999; Rutter et al. 2004a). Although the mechanism of selecting this mixed diet is not yet well understood, several explanations are still being considered, including 1) maintenance of a diverse rumen microflora (Rutter et al. 2000); 2) maintenance of some optimal carbon/nitrogen balance or ratio of rewards with type of food in the diet (Senft et al. 1987); 3) avoidance of toxic consequences of ingestion of one dietary component to excess (Provenza and Balph 1990; Provenza et al. 1992); 4) avoidance of grazing at night due to a perceived risk of predation that may influence diurnal patterns of preference (Newman et al. 1995; Gregorini et al. 2006; Chapman et al. 2007); 5) constant sampling and evaluation of familiar foods in familiar environments, as nutrient content and toxicity may vary with time (Provenza et al. 1992); and 6) resource depletion, which results in a trade-off between remaining at a patch and consuming less desirable species or plant parts, or moving on to a fresh patch of more preferred species or plant parts (Mitchell 1990).

If intake maximization was the goal during the grazing process (Arnold 1987; Ungar and Noy-Meir 1988; Illius et al. 1999), as predicted by the classical optimal foraging theory (Pyke 1984), grazing ruminants should prefer legumes over grasses, because legumes are easier to masticate and digest, thereby clearing the rumen faster (Waghorn 1986; Waghorn et al. 1989; Mtengeti et al. 1995). However, cows and sheep have consistently preferred a diet containing approximately 50–70% white clover (*Trifolium repens* L.) when offered adjacent monocultures of perennial ryegrass (*Lolium perenne* L.) and white clover, despite changes in the proportional area of the two species offered (Newman et al. 1992; Parsons et al. 1994; Rutter et al. 2004a). These preferences have shown a distinct diurnal pattern with clover being preferred in the morning with an increasing preference for grass in the afternoon (Parsons et al. 1994; Rutter et al. 2004a). This diurnal preference pattern provides support for many of the proposed mechanisms suggested in the previous paragraph. For example, grazing ruminants may increase consumption of grasses in the evening due to the higher fiber content to maintain ruminal fill overnight (Newman et al. 1995), or because the sugar content of grasses increases throughout the day, potentially making them more palatable in the afternoon compared to the morning (Mayland et al. 2005).

Grazing ruminants presented with adjacent monocultures of forage species are subjected to minimal physical constraints to selection and could therefore express preference (Hodgson 1979). In reality, grazing animals are challenged with swards that vary in time and space, which constrains animal preference and stimulates selective behavior. This decision-making process may have a significant impact on grazing time, herbage DMI, and nutrient intake pattern (Hill et al. 2009). Selective grazing behavior not only depends on sward heterogeneity, but also on changes in the sward as it is defoliated, and on the nutritional status of the animal (Rook et al. 2002). It is known that the choice of the grazing ruminant at any time depends on the past, current, and expected future nutritional states (Mangel and Clark 1986; Scott and Provenza 1999), which can be tied to the satiety hypothesis (Bailey and Provenza 2008).

As previously mentioned, grazing ruminants confront a mixed sward daily, with or without defined patches of plant species, and with spatiotemporally varying nutrients and toxins. Consequently, in a scale of a feeding site defined as arrangements of multiple patches shown within a grazing bout (Bailey et al. 1996), ruminants search for or avoid species that generate a comfortable or uncomfortable state, respectively (Forbes and Provenza 2000). Daily herbage and nutrient intake results from multiple grazing bouts; therefore, animals may integrate nutritional information from past, present, and expected future bouts in order to optimize daily nutrient intake

(Pitroff and Kothmann 1999). For example, wapiti (*Cervus elaphus*) have been shown to optimize nutrient intake by selecting specific patches of grass (Wilmshurst et al. 1995). There is also evidence that beef cattle adapt selective foraging behavior according to the crude protein (CP) level of two different grasses (Hirata et al. 2008). Moreover, bison (*Bison bison*) have been shown to select wheat sedge primarily (*Carex atherodes* Spreng.) from among seven plant species, which enables them to maximize short-term energy intake at the expense of a reduction in the long-term energy gain (Fortin et al. 2002). Bergman et al. (2001) argued that this conditioned preference shown by bison may be related to needs such as maintaining thermal balance, scanning for predators, or social status, which can be interpreted as an attempt at reaching a more stable comfortable state (Bailey and Provenza 2008). Another example of how the satiety hypothesis may help in explaining patterns of temporal selectivity is presented in recent work conducted with dairy cows (Emmick 2007). Lactating dairy cows were offered either a low (11% CP) or high (21% CP) protein supplement in the barn, then turned out onto adjacent monoculture pastures of orchardgrass (*Dactylis glomerata* L.), white clover, or a mixture of the grass and legume species, with simultaneous access to all three strips. Grazing behavior (time spent grazing, number of bites, biting rate) were visually observed in each monoculture. When fed low supplemental CP, cows spent more time grazing and took more bites of the high-protein clover relative to grass after turnout to pasture. However, when supplemental CP was high (21%, well over National Research Council [NRC 2001] recommendations), cows favored the lower-protein, higher-fiber grass relative to clover. These results and others (Orr et al. 2001) led to the hypothesis that feeding strategies may alter the diurnal pattern of preference (Newman et al. 1992; Parsons et al. 1994). Thus, graziers may be better able to manage selectivity by the grazing ruminant according to specific determined purposes, such as production of meat, fiber, or milk.

HOW DIETARY CHOICE AFFECTS PRIMARY AND SECONDARY PRODUCTIVITY

While previous research evaluated the effects of sward attributes on bite mass and DMI rate of grazing ruminants, including sward surface height (Wade et al. 1989; Laca et al. 1994; Rook et al. 1994) and sward bulk density (Laca et al. 1994), few studies have examined the effect of plant species diversity on secondary productivity (Soder et al. 2007). Of the studies that have evaluated diversity in relation to secondary productivity, almost all only examined the effect of two species mixtures consisting of a cool-season grass and legume, usually perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.). In what could be regarded as a study of relative abundance, albeit with only two species, lactating dairy cows offered grass pastures containing 25%, 50%, or 75% clover increased DMI by 8%, 23%, and 30%, respectively, when compared with cows grazing a grass monoculture (Harris et al. 1997). Daily milk yield for cows grazing the 50% and 75% clover was similar, and milk yield was 33% greater than the grass monoculture. Cows grazing the 75% clover swards may have incurred a "protein penalty" (i.e., incurred an extra energy cost to metabolize excess protein in the legume-dominant sward) explaining, in part, why milk yield responses to increased clover content were nonlinear. A similar study (Yarrow and Penning 2001) in which perennial ryegrass–white clover swards were managed to produce different clover proportions and then continuously stocked with beef cattle also showed animal responses to clover proportion, but differences were difficult to maintain as, under common management, all swards converged to have the same proportion of clover.

Grazing research with lactating dairy cows in the mid-1960s indicated that there was no increase in milk production with complex pasture mixtures of grasses and legumes (Wedin et al. 1965). Phillips and James (1998) showed that dairy cows grazing a mixed sward of white clover and perennial ryegrass had greater milk yield (22.1 $kg \cdot cow^{-1} \cdot d^{-1}$) than cows that grazed a ryegrass monoculture (18.9 $kg \cdot cow^{-1} \cdot d^{-1}$). However, when offered a choice of the perennial ryegrass monoculture and the mixed sward of white clover and perennial ryegrass, cows failed to select a diet that supported higher milk yield (20.0 $kg \cdot cow^{-1} \cdot d^{-1}$). The tendency for longer grazing times and the lower stocking rates of the cows in the choice treatment suggests that utilization of the pastures may have been less efficient than for the monoculture treatments (Phillips and James 1998).

Recent research (Sanderson et al. 2005; Soder et al. 2006) conducted in a rotational dairy grazing system with a range of swards of different species richness, from an orchardgrass-white clover mixture to a complex sward containing nine species (grasses, legumes, and *Cichorium intybus* [chicory]), showed several important trends. First, herbage production per hectare as assessed by grazing (with mechanical clipping of excess growth when necessary) did not differ significantly between 3, 6, and 9 species swards, but was significantly greater (58%) for these swards compared to the 2 species grass–legume mixture during a dry year but not during a wet year (12% difference). Secondly, milk produced per hectare did not differ significantly between 3, 6, or 9 species swards but was 86% higher for these swards than for the orchardgrass–white clover mixture during the dry year, and 34% higher during the wetter year. These differences in milk yield per hectare arose from differences in stocking rates rather than from daily milk yield per cow, which did not differ significantly across the treatments. This lack of effect on milk yield per cow was supported by the lack of differences in ingestive grazing behavior (grazing time, biting rate, and grazing jaw movements measured using the procedures of Rutter et al. [1997b]) and herbage DMI (Soder et al. 2006). One possible explanation is that these lactating animals had a high intake drive, which made them less selective (NRC 2001; Rutter et al. 1997c).

Research concerning the effects of pasture mixtures on primary and secondary productivity is still in the early stages; therefore practical recommendations for farmers are not yet available. Evidence exists that, in improved temperate grazing systems, more complex pasture mixtures can improve primary production, reduce weed invasion, and improve system resilience to climatic extremes such as drought (Skinner et al. 2004; Sanderson et al. 2005), which are important considerations for farmers. There is also some evidence that where improvements in primary production are observed, it is reflected in greater total animal production per hectare, which is clearly of benefit to producers. However, the costs and practicality of using more complex pasture mixtures and their sustainability in the longer term must be taken into account.

The effects of greater pasture complexity at an individual animal level are more unclear, and further research is needed in this area. Additional research is required regarding the agronomic feasibility of establishing and maintaining multiple species pastures. Finally, there is a need for continued study of the interactions between pasture mixtures and sward type and animal management regimes.

CHARACTERIZING DIETARY SELECTION—CURRENT METHODOLOGIES

Estimating intake and diet selection of grazing ruminants is challenging because of the extensive situations of pastures (compared with confinement) and the choices offered to grazing ruminants compared with confined animals fed a precise diet. However, methodologies for estimating diet selection and composition in grazing ruminants have been developed and utilized for several decades (Holechek et al. 1982; Norbury and Sanson 1992). This section will provide information about techniques and experimental models that were developed in the past, as well as those that were developed more recently.

Utilization Technique and Visual Observation of the Animal

Although different methods have been used to quantify utilization, one of the most common methodologies is to measure percentage weight removal by taking pre- and postgrazing clippings. Estimating utilization allows the researcher to determine quickly where and to what extent a pasture is being grazed. The major disadvantages with any utilization technique are that 1) information regarding when and how often a forage species was used is not available; 2) herbage regrowth during the grazing period can make accurate estimates of utilization difficult; and 3) large-scale losses of plant parts from weathering, trampling, and wildlife grazing can greatly affect the final results (Cook and Stoddart 1953).

Direct observation of the grazing animal has been a widely used procedure in past and present studies of the dietary botanical composition of ruminants and involves an observer following a grazing animal and documenting the relative amounts and types of different forage species being consumed (Theurer 1970; Theurer et al. 1976; Hassoun 2002; Rutter et al. 2004a). Simplicity, few equipment requirements, and ease of use are major advantages of direct observation. However, major issues arise when the observer tried to identify species and quantify how much of a plant was consumed. Quantitative information from direct observation has been obtained from two different approaches, such as the bite-count and feeding-minutes techniques. The bite-count procedure differs from the latter in that number of bites taken from each plant species is recorded rather than the length of grazing time (Reppert 1960). Factors influencing the accuracy and precision of the direct observation procedure include the degree of training of the observer, complexity of the plant community present, and/or phenological development of individual plants.

More recently, electronic behavior recorders were developed (Champion et al. 1997; Rutter et al. 1997b; Scheibe et al. 1998), which allows independence from an observer, thereby improving accuracy and precision of bite counting, grazing time, and other activities. The data obtained with the recorder developed by Rutter et al. (1997b) are analyzed with a software program called GRAZE (Rutter 2000). Selective grazing behavior has been successfully monitored by using this device in sheep (Orr et al. 2003; Champion et al. 2004), beef cattle (Orr et al. 2005a; Boland et al. 2007), and dairy cows (Orr et al. 2001; Soder et al. 2006). The use of this device has allowed estimation of intake rates, including evidence that intake rates of grasses and legumes differ (Rutter et al. 2004a, 2004b). The system developed by Scheibe et al. (1998) can be used for automatic recording of different patterns of behavior, such as activity and feeding. It was found to be more suitable for determination of diurnal patterns, change over time, and relative comparison between behavior levels than it actually was for measurement of absolute duration of a given behavior. These findings, in combination with other techniques, can be used to estimate the diet composition of the grazing ruminant. The combination of the electronic device developed by Rutter et al. (1997b) with, for example, the alkane technique (described below) will allow the amount of legume and/or grass consumed by the animal in a simple sward to be quantified.

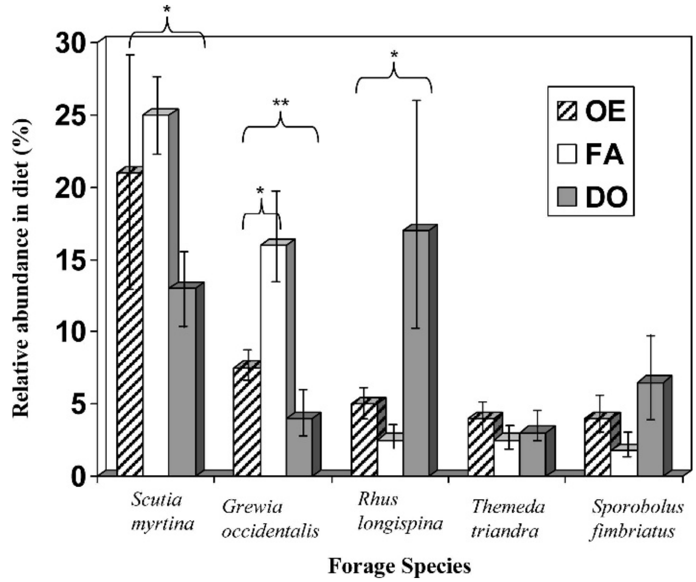

Figure 1. Comparison of mean relative abundance (%), with SE, of five common forage species found in Boer goats grazing South African range recorded by direct observation (DO), fecal analysis (FA), and esophageal extrusa (OE). Significant differences between techniques are indicated (*$P < 0.005$, **$P < 0.01$). Adapted from Henley et al. (2001).

Surgically Modified Animals, Stomach Content, and Fecal Sample Analyses

Esophageal and ruminal fistula techniques have considerable advantage over the sampling methods previously discussed, because grazed herbage samples can be obtained directly. Although the esophageal fistula was used widely in domestic animals to collect ingested feeds before entering the rumen, the surgery was difficult and success was variable (Van Dyne and Torrell 1964; Theurer 1970; Theurer et al. 1976; Henley et al. 2001; Fig. 1). Increased success rate of the surgery in ruminally fistulated animals (Lesperance et al. 1960; Theurer et al. 1976) and the ease of maintaining and sampling a ruminally cannulated animal versus the cost and the intensive labor involved in maintaining an esophageally cannulated animal made the ruminal fistulas the preferred tool in nutrition studies.

A common procedure used by wildlife researchers for estimating diet composition is stomach and intestinal tract analysis, wherein the gastrointestinal tract is harvested and dissected, and its contents are examined for botanical composition (Chippendale 1962; Chamrad and Box 1968; Smith and Shandruk 1979). The main disadvantage of this procedure is that it involves sacrifice of animals and, therefore, is restricted primarily to wild animals with large populations. Other major disadvantages are that differential levels of destruction of forage species during digestion alter the proportions of the food items consumed (Vavra and Holechek 1980), and the location where the forage was consumed cannot be determined. From the 1960s to the 1990s research was conducted in the estimation of diet composition through the analyses of feces (Sanders et al. 1980; Glasser et al. 2008). Advantages of the fecal analysis technique included 1) samples could be collected with minimal field work, 2) the technique worked for both domestic and wild animals, 3) the technique was not limited by weather or rough terrain, and 4) fecal analysis was not subject to observer bias. Other work found this fecal-analysis technique to be time consuming, to require laboratory facilities and experience, and to provide questionable accuracy (Smith and Shandruck 1979).

Spatially Separated Pastures (Adjacent Monocultures)

Animals grazing a two-species pasture consisting of a grass and a legume need to search for their preferred forage within the mixture. This physical constraint will, to some extent, affect animal decision making, leading to selective behavior strategies. However, if researchers wish to study what animals prefer, then selection must be measured in a situation with minimal or no physical constraints (Newman et al. 1995). This situation is achieved by grazing those two herbage species as spatially separate but adjacent monocultures. In that situation, animals are given an unconstrained choice to graze either grass or clover whenever they desire. Sheep and cattle show a partial preference for clover of about 70% when grazing adjacent monocultures of white clover and perennial ryegrass (Rutter 2006). This observation of partial preference not only is the same for cattle and sheep (Parsons et al. 1994; Rutter et al. 1999), but also for different ratios of grass and clover offered (Parsons et al. 1994; Rutter et al. 2004a, 2004b), and different heights of legumes vs. grasses (Harvey et al. 2000).

Microsward Technique

Microswards provide a high degree of control over uniformity of sward structure, providing the possibility of an in-depth study of grazing behavior. With the microsward technique, Black and Kenney (1984) were able to separate the effects of sward height and bulk density without confounding effects of season, herbage quality, or animal status, a significant accomplishment. Later, other small-scale intake assessment methodologies were used, including microswards in the field (Burlison et al. 1991), artificially created sward boards (Laca et al. 1992), or turves cut from pasture and placed in trays (Newman et al. 1992). Orr et al. (2005b) developed microsward boxes with the objective of developing and testing a low-cost methodology to screen forage attributes when offered in boxes. Similarly, Ginane and Dumont (2006) developed cultivated pots ($0.39\,0.315 \times 0.26$ m) to study conditioned food aversion in grazing conditions. The bottom of the pots was perforated to let water flow out. Although the microsward boxes were developed for testing forage characteristics that could be used in breeding programs, they can also be used for comparing bite dimensions across monocultures (Soder and Sanderson 2007) and potentially to measure dietary choice at a feeding-station level. However, we are not aware of any data published dealing with the latter issue. It must be recognized that the microsward box technique has its drawbacks, including 1) the animal is removed from its natural foraging context, 2) the forage presented to the animal often deviates from anything that the animal is likely to encounter naturally, and 3) due to the microsward size, there are restrictions on the duration of an observation (Ungar 1996).

n-Alkanes to Estimate Diet Composition

Hydrocarbons are present in the waxes of many higher plants, with *n*-alkanes being the most common of them (Dove and Mayes 2005). Differences between species in individual alkane concentrations enable the botanical composition of herbage mixtures to be calculated, whether these mixtures be harvested forage, extrusa samples, or diets of grazing ruminants as reflected in their feces (Coates and Penning 2000). The principle of using alkanes to estimate diet composition is the same as for other chemical approaches; that is, the composition of a representative sample of a mixture of forages (extrusas, digesta, or feces) is determined from knowledge of the concentrations of the chemical markers in the mixture and in the components that make up the mixture (Dove and Mayes 1996).

The alkanes of herbage and feces have been used with grazing ruminants to estimate diet composition in situations in which the diet consisted of two dietary components (Armstrong et al. 1993). When used with mixed swards, the alkane method has been shown to distinguish up to four component plant species (Dove and Mayes 1996).

In more diverse swards there are usually more plant species available for consumption than there are alkanes to discriminate them. In this case different approaches can be taken: 1) decrease the number of dietary components by grouping species in the diet (e.g., grasses, legumes, and browse) or pooling species with similar *n*-alkanes profiles for statistical analyses; 2) combining the use of alkanes with other techniques such as microhistological examination of esophageal extrusa (Salt et al. 1994) to estimate dietary components; 3) using other mathematical approaches in the use of *n*-alkanes as markers (Barcia et al. 2007); or 4) using additional diet composition markers in plant wax: alkenes (unsaturated aliphatic hydrocarbons), long-chain alcohols (Bughalo et al. 2004; Fraser et al. 2006), and long chain fatty acids (Ali et al. 2004, 2005). These components also have different concentrations in the different plant species and plant parts and can be obtained together with alkanes as part of the same analytical procedure (Dove and Mayes 2006).

Tracking Animal Movements in Small and Large Scale

Different spatial and temporal distributions of defoliation affect spatial heterogeneity and hence the potential for yield and stability of a particular pasture (Parsons and Dumont 2003). Although previous studies measured bite dimensions (depth and area) with the use of artificial swards (Laca et al. 1992) or in the field (Edwards et al. 1995), a method was developed to determine bite dimensions and movement patterns of cattle and sheep grazing a spatially homogeneous sward (Rook et al. 2004). In this study it was determined that sheep and cattle had an innate spatial method for exploring and exploiting the vegetation, hence affecting dietary choices. Because distance traveled between grazing bouts and width of the defoliated area were much smaller for sheep than for cattle, it was concluded that sheep created a smaller scale of imprint on the vegetation.

The variety of global positioning system (GPS) configurations now available to researchers makes it possible to apply this technology to most resource-selection studies of mammals and some large birds. Research on the ecology and management of grazing systems using sheep (Rutter et al. 1997a; Hulbert et al. 1998) and cattle (Turner et al. 2000; Ganskopp 2001) has also incorporated the use of GPS tracking collars. Size of animal and size and cost of GPS units are the key issues that researchers must consider in selecting an appropriate system to meet their research objectives. Attention must also be given to the operating life, accuracy of locations, and sampling intensity offered by different systems. Detailed descriptions of the concept of GPS technology are given by several authors (Moen et al. 1997; Rempel and Rodgers 1997; Rutter et al. 1997a; Hulbert et al. 1998; Turner et al. 2000).

The study of landscape use by animals requires a record of the location of individuals over time. Technical and logistic difficulties in obtaining and collating such data have hampered the study of free-ranging animals in a spatially explicit way (Coughenour 1991; Turner et al. 2000). Furthermore, a considerable portion of foraging activity takes place at night (Hulbert et al. 1998). Thus, GPS technology can provide a suitable solution because it allows long-term, uninterrupted monitoring of grazing animals at relatively lower cost. Tracking animals using GPS represents a major advance in spatiotemporal data acquisition.

By using GPS units in conjunction with geographic information systems, animal distribution and movement can be related to landscape features. For example, Ganskopp (2001) used this technology to evaluate the impact of salt and water manipulations in affecting cattle distribution. Foraging ecology inferences can be made by pairing animal-location data with associated animal-activity data (Hessle et al. 2007). The accuracy and precision of location estimates has improved 10-fold since the first GPS-based telemetry systems were introduced and even greater accuracy may be achieved in the next few years.

Mapping Vegetation

The simplest approach to vegetation mapping is through manual survey. If the map has references to features, then the approach is very easy, although featureless terrain requires the use of highly accurate equipment. Rutter et al. (2006) used precise GPS receivers, allowing for a more rapid entry of vegetation types into a hand-held GPS receiver automatically recording the observer's location. Although tracking animals with the use of submeter GPS is possible, there is not the same precision as with vegetation mapping (Rutter et al. 2006), where there is a need to reduce the distance between vegetation samples, increasing time, effort, and the numbers of samples needed. Based on his own experience, Rutter (2007) estimated that in a single 1.5-ha paddock sampled in a grid at 4-m intervals there are 950 points; approximately 8 h would be required to map that paddock. If samples are taken every 0.25 m (so that precision is increased) then there are 240 000 sample points, and 50 working weeks ($8\ h \cdot d^{-1}$, $5\ d \cdot wk^{-1}$) are needed to complete the mapping. Aerial imagery and high-resolution satellite imagery (although not inexpensive) can provide the opportunity to generate precise vegetation maps (Rutter 2007).

Bioacoustics

Alkon and Cohen (1986) and Alkon et al. (1989) first proposed the use of acoustic biotelemetry for animal-behavior studies because of the rich information contained in sound records. Lee et al. (1988) considered this method as a noninvasive method to study the manipulation of feed inside the mouth. Acoustics was used to monitor jaw movement activity in cattle during short-duration grazing trials with an inward-facing microphone mounted on the forehead of the animal. This type of acoustic monitoring revealed a new type of jaw movement named the "chew-bite" whereby herbage already in the mouth is chewed and fresh herbage is severed in the course of a single jaw movement (Laca et al. 1992, 1994). Clapham et al. (2006) used solid-state microphones and discrete ultra-high-frequency transmitters that were attached to halters fitted to steers. Corresponding receivers were mounted on digital video cameras to allow synchronized audio and video recording of grazing behavior. Grazing and ruminating cattle were recorded over a number of 120-min periods throughout the summer. Grazing events were classified by matching sound wave and video events from the tapes. The audio file was subjected to spectral analysis. The results of this study suggest that sound analysis can be used to quantify and discriminate ingestive behaviors.

Galli et al. (2006) found that fresh forage was chewed more than dry hay when fed to steers, with no difference between fresh alfalfa and fresh grass, and Alfalfa hay was chewed less than grass hay. This demonstrated that chewing was primarily affected by water content of the forage, and that internal water content could be considered as a potential tool for promoting chewing without reducing diet quality.

IMPLICATIONS

This review has revealed that a rich literature on dietary selection by grazing animals exists. Nevertheless, there are a number of areas where further research is urgently needed. Much of the work on dietary selection and preference has been based on simple model systems, often involving a choice between only two herbage species. These have provided a vital tool to allow understanding of the fundamental principles of foraging behavior. In reality, however, grazing ruminants are often faced with much more complex situations. For example, sward surveys in the northeastern United States have shown that the average pasture contains more than 20 plant species (Tracy and Sanderson 2000; Sanderson et al. 2005). It is therefore important that the robustness of earlier conclusions from model systems is tested in these more realistic scenarios.

Fortunately, some of the methodological developments discussed above now offer the potential to undertake such studies to an acceptable degree of accuracy within the resources likely to be available.

As discussed above, one of the principal benefits ascribed to increased plant diversity in grassland systems has been increased primary productivity. There is also some evidence of benefits to secondary productivity and to other functional attributes such as product quality and sward stability. However, studies of this secondary functionality have so far been limited and further work is needed given the increased emphasis placed on these functions by consumers. Further additional functions such as impacts on water quality and wildlife diversity will also need to be considered as the demands for agriculture to be multifunctional increase.

In addition to the more applied research discussed above, there will be a need to continue to understand the fundamental principles that underlie animal choices. Key issues include a better linking of behavioral and nutritional studies and the development of more explicit spatial models of foraging behavior that incorporate multiple scales of decision making (Laca 2009), a better understanding of the genetic factors influencing dietary selection, and a better grasp of how learning affects dietary choice (Villalba and Provenza 2009). However, these are in some way adjuncts to the central question that continues to elude researchers and that is why animals make the decisions they do. Much more effort is needed to identify the key currencies that animals are using to make their choices, including nonnutritional factors, and the trade-offs between currencies that lead to the final foraging choice. This review has demonstrated that, despite the complexities of dietary choice and the substantial methodological issues that arise, considerable progress in understanding dietary choice has been made. These results, coupled with considerable methodological breakthroughs, provide a firm basis for further progress in this important area.

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