Preferences of lambs offered Italian ryegrass (*Lolium multiflorum* L.) and barley (*Hordeum vulgare* L.) herbage as choices

F. Catanese*†, R. A. Distel*† and M. Arzadún‡

*Centro de Recursos Naturales Renovables de la Zona Semiárida (CERZOS), Consejo Nacional de Investigaciones Científicas y Técnicas de la República, Argentina, †Departamento de Agronomía, Universidad Nacional del Sur, Bahía Blanca, Argentina, and ‡Campo Experimental Coronel Suárez, Ministerio de Asuntos Agrarios de la Provincia de Buenos Aires, Bahia Blanca, Argentina

Abstract

Partial preference for feeds in ruminants is a well-documented phenomenon although their explanation can be elusive. The hypothesis was tested that sheep offered herbage of two annual grass species differing in chemical composition free-choice would select a diet that would maximize the nutritive value of the diet compared with sheep offered each herbage separately through a greater nutrient balance and synchronization of nutrient release for efficient ruminal microbial function. Fifteen male lambs were placed into metabolic cages, and randomly assigned to three treatments (n = 5): Italian ryegrass fresh herbage (treatment R), barley fresh herbage (treatment B) or free-choice Italian ryegrass and barley fresh herbage (treatment RB). Both herbages had similar crude protein concentrations but Italian ryegrass herbage had higher concentration of water-soluble carbohydrates and lower concentration of fibre than barley herbage. Lambs were exposed to the treatments for 15 d. Lambs on treatment RB showed a partial preference of 0·82 (s.e. 0·031) for Italian ryegrass. Lambs on treatment RB had higher intakes of digestible dry matter and higher values for nitrogen retention than lambs on treatment B although similar to that of lambs on treatment R. The results for the dietary choices were not always consistent with maximizing the nutritive value of the diet. Other explanations, such as lambs needed to sample and track the nutritive value of dietary options or there was the development of transient food aversions, were also possible.

Correspondence to: Roberto A. Distel, Departamento de Agronomía y CERZOS, Universidad Nacional del Sur, San Andrés 800 8000, Bahía Blanca, Argentina.
E-mail: cedistel@criba.edu.ar

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Introduction

Diet selection by mammalian herbivores is often approached within the framework of optimal foraging theory (Stephens and Krebs, 1986). This theory assumes that herbivores are capable of assessing the nutritive value of a feed and that they forage to maximize energy intake per unit effort. Accordingly, herbivores should not exhibit partial preferences for high quality foods in a choice situation with foods of lower nutritional quality. However, partial preferences and mixed diets are commonly observed in many species in both grazing experiments (Cortes *et al.*, 2006; Hirata *et al.*, 2008) and controlled feeding experiments (Berteaux *et al.*, 1998; Fisher *et al.*, 1999; Illius *et al.*, 1999; Ginane *et al.*, 2002). For example, studies on diet selection by sheep and cattle in choice situations involving grasses and white clover have consistently shown a partial preference of approximately 0·70 for white clover, the species with a higher nutritive value (Rutter, 2006).

Among plausible explanations to account for partial preferences in herbivores one is the attempt to meet nutritional needs (Westoby, 1978; Newman *et al.*, 1992; Provenza *et al.*, 2003; Simpson *et al.*, 2004). The influence of animal physiological state and recent diet on dietary choices (Newman *et al.*, 1994; Parsons *et al.*, 1994; Ginane *et al.*, 2002) provides some evidence to support this hypothesis. However, little research has been conducted with ruminants to explore the nutritive value of mixed diets in choice experiments, particularly when offered grass herbage. A mixed diet may improve digestive outcomes by providing a greater nutrient balance and synchronization of nutrient release for efficient ruminal microbial function (Kyriazakis and

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Oldham, 1997; Provenza *et al.*, 2003; Rutter, 2006) compared to a single herbage.

The hypothesis was tested that lambs, offered two winter annual grasses differing in nutritive value as free choices, would select a mixed diet that would enhance digestive outcomes, compared with sheep fed each species offered separately. It was predicted that there would be a higher intake of digestible dry matter and nitrogen (N) retention in sheep fed free-choice Italian ryegrass and barley herbage than in sheep fed each grass species separately.

Materials and methods

The experiment was conducted at the Research Station of the Buenos Aires Agriculture Ministry, located in Pasman, Argentina (37°11′S; 62°08′W). All maintenance and experimental protocols fulfilled animal welfare regulations of the Universidad Nacional del Sur, Bahía Blanca, Argentina.

Lambs and housing

Fifteen Corriedale male lambs [mean 29 (standard deviation of mean, 2·6) kg] were placed in individual metabolic cages located indoors after having grazed on wheat at a vegetative stage for the preceding 30 d. Metabolic cages were provided with two feed bins (10 L each) and an automatic water dispenser (1 L). Cages also collected urine and faeces separately. The size of the cages prevented lambs from turning around although they had enough space to eat, drink and lie while resting.

Treatments and experimental procedures

Italian ryegrass (*Lolium multiflorum* L. cv. *Eclipse*, hereafter referred to as ryegrass) and barley (*Hordeum vulgare* L. cv. *Alicia*) were sown on 15 February, 2006. The ryegrass cultivar was specially selected for having relatively high concentration of water-soluble carbohydrates and relatively low concentrations of fibre in herbage compared with that of barley herbage (Freddi *et al.*, 2001).

The experiment started on 10 July 2006 when ryegrass and barley were in a vegetative stage. Lambs were assigned randomly to three treatments ($n = 5$). Treatments consisted of offering lambs ryegrass herbage (treatment R), barley herbage (treatment B) or a free choice of ryegrass and barley herbage (treatment RB). The lambs had no previous experience of these forages that could affect preference or intake in the present study (see Provenza, 1995). They were exposed to the treatments for 15 d. The first 5 d were for adaptation to experimental conditions, and the next 10 d for measurements to be made.

Ryegrass and barley herbage was harvested daily in the afternoon and stored indoors overnight at room temperature. Since room temperature was close to ambient temperature, and winter nights were cold (frosts are common) at the study site, it can reasonably be assumed no major change in the chemical composition of the herbage occurred during overnight storage. The following day, at 07:00 h, both herbages were chopped into a similar particle length (3–4 cm), and stored at 4°C. All lambs were offered herbage at 08:00, 11:00, 15:00 and 18:00 h with 1200 g of ryegrass, 1200 g of barley or 1200 g of both herbages in separate feed bins. This ensured continuous availability of herbage *ad libitum* and allowed at least 20% refusals. At 22:00 h, refusals from all the lambs were collected and weighed. Herbage intake was measured daily as the difference between offered and refused herbage and expressed on a dry matter (DM) basis. From 22:00 h to 08:00 h on the next morning, lambs received no herbage.

On the first day of the feeding experiment, the position of the herbage in the feed bins on treatment RB was randomized. Thereafter, position was not changed. Although position can influence some behaviours (e.g. decisions when no previous information of food location is provided, or when exploring the environment for first time; Hosoi *et al.*, 1995), research has demonstrated that ruminants can be efficient at learning the associations between food sensorial characteristics and its post-ingestive consequences (Forbes and Kyriazakis, 1995; Provenza, 1995). Several authors have observed that food position does not affect feed preferences and diet selection (Hou, 1991; Hou *et al.*, 1991; Ganskopp, 1995; James *et al.*, 2001).

Each herbage offered was thoroughly mixed and sampled (100 g) on each feeding occasion (i.e. 08:00, 11:00, 15:00 and 18:00 h). Daily samples were pooled and stored at −18°C until laboratory analyses. The same procedure was repeated for refusals of each herbage.

Faeces and urine were weighed daily at 10:00 h throughout the measurement period. Urine was collected into 200 mL of a hydrochloric acid solution (5 mL L^{-1}) to prevent ammonia volatilization. Samples of urine (0·05 of total volume) and faeces (0·10 of total weight) were collected daily, a representative sample taken, and these samples were pooled for the measurement period. Samples were stored at −18°C until laboratory analyses.

Laboratory analyses

Pooled samples of offered and refused forages were freeze − dried to a constant weight for the determination of DM = content. Samples of offered forages were then ground to pass through a 1-mm screen (Wiley

Mill; Thomas Scientific, Swedesboro, NJ, USA) and analyzed for concentrations of crude protein (CP, AOAC, 1990), neutral-detergent fibre (NDF, Goering and Van Soest, 1970) and water-soluble carbohydrates (WSC, Barnett and Millar, 1950).

Faecal samples were oven dried at 65°C to constant weight to determine DM content, and then ground to pass through a 1-mm screen. Faecal samples were analyzed for N concentration (AOAC, 1990) and for NDF concentration (Goering and Van Soest, 1970). Urine samples were analysed for N concentration (AOAC, 1990).

Table 1 Dry matter (DM) content and concentration of crude protein (CP), neutral-detergent fibre (NDF) and water-soluble carbohydrates (WSC) in ryegrass and barley herbage.

Variable	Herbage		s.e. of mean
	Ryegrass	Barley	
DM content (g kg^{-1})	243·0	262·0	7·0
CP concentration (g kg^{-1} DM)	171·9	158·5	6·7
NDF concentration (g kg^{-1} DM)	502·4	557·0	9·9
WSC concentration (g kg^{-1} DM)	299·8	186·0	9·1

Statistical analyses

Dry matter intake and intake of digestible DM data were analysed using a completely randomized design with repeated measures for the analysis of variance. Lambs were the experimental unit and day was the repeated measure. All ANOVA analyses were performed using the PROC MIXED procedure of SAS (2000). Fixed effects of the model were treatment, day and day × treatment interaction. Lambs were the random term. The within-lamb covariance matrix was modelled with a compound symmetric structure which proved to have the best fit according to Schwarz's Bayesian criterion (Littell *et al.*, 1998). Digestibility of DM, NDF digestibility, N intake, N excreted in faeces, N excreted in urine, total N excreted, N retention and proportion of N retained were analysed using a completely randomized design for the analysis of variance. For these variables, ANOVA analyses were performed using the one-way ANOVA statistical package of SAS (2000). When a significant difference occurred ($P < 0{\cdot}05$), means were compared using the Tukey–Kramer test.

Results

Chemical composition of herbage

Herbage of ryegrass and barley had a similar content of DM and concentration of CP, but differed in NDF and WSC concentrations (Table 1). Concentration of NDF was higher in barley than in ryegrass herbage whereas WSC concentration was higher in the latter than in the former species.

Intake and digestibility of dry matter and diet composition

Intake of DM did not differ among treatments (Table 2). Mean intake of DM on days 6 and 8 was lower ($P < 0{\cdot}05$) than for the rest of the days (Figure 1). There was also a significant interaction of treatment × day ($P < 0{\cdot}001$). On treatment R, mean intake of DM on days 6 and 8 was lower ($P < 0{\cdot}05$) than for the rest of the experimental period. On treatments B and RB, mean intake of DM did not change significantly across experimental days. Lambs on treatment RB showed a higher preference for ryegrass [proportion in diet, 0·82 (s.e. of mean, 3·2); Figure 2].

Digestibility of DM and intake of digestible DM were similar on treatments RB and R, and higher than on treatment B ($P < 0{\cdot}01$ and $P < 0{\cdot}05$ respectively; Table 2). There was a significant day ($P < 0{\cdot}001$) and day × treatment ($P < 0{\cdot}005$) interaction for intake of digestible DM. Digestibility of NDF was higher ($P < 0{\cdot}05$) on treatment R than treatment B, whereas digestibility of NDF on treatment RB did not differ from treatments R and B (Table 2).

Nitrogen balance

There were no differences between treatments in N intake, excretion of N in faeces and excretion of N in urine (Table 2). On the other hand, the N retention and the proportion of N retained were higher on treatment R and RB than on treatment B ($P < 0{\cdot}01$; Table 2).

Discussion

The results of this study should be considered against the background of the small number of lambs per treatment ($n = 5$) in view of marked inter-individual variability in food preferences that can occur (e.g. Scott and Provenza, 1999; Prache *et al.*, 2006) although the between-lamb variability in this study within a treatment was not large.

In the free-choice treatment (treatment RB), lambs showed a partial preference of 0·82 for ryegrass herbage and of 0·18 for barley herbage, which was in agreement with other studies on the preference by sheep for herbages with a high non-structural carbohydrates concentration (Fisher *et al.*, 1999; Cortes *et al.*, 2006). High concentrations of water-soluble carbohydrates

Table 2 Intake, digestibility and nitrogen balance by lambs offered barley herbage (treatment B), ryegrass herbage (treatment R) or free-choice ryegrass and barley herbages (treatment RB) (n = 5).

	Treatment				
Variable	**B**	**R**	**RB**	**s.e. of mean**	**Level of significance**
DM intake (g d^{-1} kg^{-1} LW)	64·73	64·93	62·78	2·88	NS
Intake of digestible DM (g d^{-1} kg^{-1} LW)	42·83[b]†	50·81[a]	47·15[a]	1·96	*
Nitrogen (N) intake (g d^{-1})	21·42	21·21	19·89	1·36	NS
Digestibility of DM	0·661[b]	0·783[a]	0·759[a]	0·0011	**
Digestibility of NDF	0·695[b]	0·786[a]	0·765[ab]	0·0190	*
N excretion in faeces (g d^{-1})	7·53	5·90	5·60	0·59	NS
N excretion in urine (g d^{-1})	12·24	10·05	9·64	0·99	NS
N excreted (g d^{-1})	19·77	15·65	15·54	1·47	NS
N retention (g d^{-1})	1·64[b]	5·57[a]	4·35[a]	0·66	**
Proportion on N intake retained	0·074[b]	0·265[a]	0·227[a]	0·0352	**

†Values in a row that do not share common superscript letter differ significantly at $P < 0·05$.
NS, not significant; *, $P < 0·05$; **, $P < 0·01$.

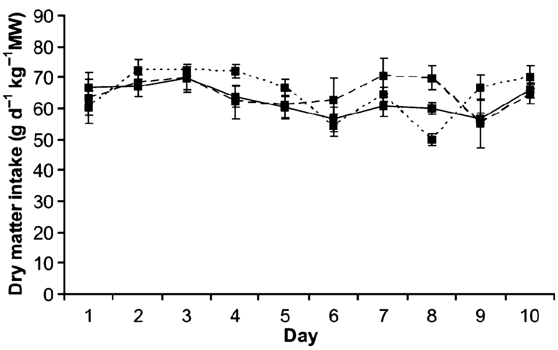

Figure 1 Dry matter intakes by lambs (n = 5) offered barley herbage (– –■– –), ryegrass herbage (- -■- -) or a free choice of barley and ryegrass herbages (—■—). The bars represent the s.e. of mean.

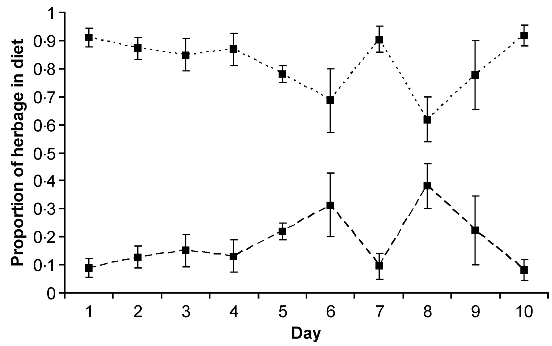

Figure 2 Preference of lambs (n = 5) for ryegrass herbage (- -■- -) when offered in a free-choice situation with barley herbage (– –■– –). The bars represent the s.e. of mean.

increase ruminal microbial protein synthesis and digestibility, and reduce urinary excretion of N (Dove and Milne, 1994; Moorby *et al.*, 2006), which may have contributed to the higher N retention in lambs offered ryegrass herbage than in lambs offered barley herbage. Although lambs offered either ryegrass or barley herbage did not differ in N intake, the relatively low DM digestibility and water-soluble carbohydrates concentration of the latter species may have contributed to lower N retention in lambs fed only the barley herbage. However, the free-choice treatment did not offer additional advantages in terms of N retention or intake of digestible DM over those lambs offered only the ryegrass herbage, undermining the hypothesis that partial preferences lead to enhanced intake of digestible DM and N retention. Sheep offered free-choice clover and ryegrass selected a mixture of them (partial preference of approximately 0·70 for clover; Rutter, 2006) even though greater intake rates (Parsons *et al.*, 1994) and performance (Gibb and Treacher, 1984; Davies *et al.*, 1992) would have been obtained by selecting only clover. In the rest of the discussion, the results are interpreted in the light of alternative hypotheses that have been proposed to explain partial preferences in ruminants.

It has been argued that ruminants have partial preferences and select mixed diets in order to maintain adequate rumen function (Rutter *et al.*, 2000). Nutrient intake in ruminants depends on maintaining a stable and healthy ruminal environment which, in turn, depends on ingesting a minimum quantity of fibre (Russell *et al.*, 1992). This does not appear to be a plausible explanation for the results in this study since lambs maintained an adequate provision of fibre even ingesting ryegrass only. On the other hand, ingestion of high quality forages, such as ryegrass, could generate ruminal pH values below those required to ensure optimal fibre digestion (Wales *et al.*, 2004). However, treatment RB did not increase either DM or NDF digestibility when compared with treatment R.

Alternatively, ruminants may need to sample dietary options in order to gain current information on their nutritive value (Illius and Gordon, 1990), leading to partial preferences. Nutritive value of herbage shows wide spatial and temporal variability (O'Reagain and Schwartz, 1995) and, therefore, this behaviour could have an adaptive value. Nonetheless, lambs on treatment RB maintained a relatively constant inclusion of barley herbage in their diet which seems at first a too high frequency of sampling for a simple choice situation between two herbages. Changes in ingestive behaviour of sheep between days, however, occurred during the present experiment, providing some evidence to support the 'sampling hypothesis'. On days 5 and 7 of the measurement period, strong dry and warm winds (velocity 53 km h^{-1}, relative humidity 18%, temperature 25°C) reduced the moisture content of ryegrass herbage giving it a 'wilted' appearance which was not observed with the barley herbage. This was associated with a reduction in the intake of ryegrass herbage on days 6 (herbage harvested on day 5) and day 8 (herbage harvested on day 7). Concomitantly, lambs on treatment RB increased the proportion of barley herbage but maintained a constant DM intake.

Partial preferences have also been attributed to transient aversions to toxic foods, unbalanced foods or balanced foods eaten too often or in excess (Provenza, 1995, 1996) which generate cyclical patterns of food intake that foster diet diversity (Provenza *et al.*, 2003). In the present study, lambs could have developed a transient food aversion for ryegrass herbage as consumption progressed during the day. Although the diurnal selection pattern on treatment RB was not measured, it was observed that lambs consumed almost exclusively ryegrass herbage in the morning and increased their consumption of barley herbage in the afternoon. A similar diurnal pattern of preference for clover in the morning and for ryegrass in the afternoon has been observed (Rutter, 2006) which has been attributed to development of transient aversion to the legume due to excess of cyanogenic glycosides, organic acids and ammonia (Provenza *et al.*, 2003).

Conclusions

Lambs fed free-choice ryegrass and barley herbage showed a partial preference of 0·82 for ryegrass and 0·18 for barley herbage. The mixed diet did not enhance intake of digestible DM or N retention, compared with lambs offered ryegrass herbage only, but increased N retention compared to the barley herbage. The results for the dietary choices were, thus, not always consistent with maximizing the nutritive value of the diet. A need to sample and track the nutritive value of dietary options, and the development of transient food aversions are possible explanations for the dietary choices made.

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References

AOAC (1990) *Official methods of analysis*. 15th edn. pp. 1230. Arlington, USA: Association of Official Analytical Chemists.

Barnett Y.A.J.G. and Millar T.B. (1950) The determination of soluble carbohydrates in dried sample of grass silage by anthrone method. *Journal of the Science of Food and Agriculture*, **1**, 336–339.

Berteaux D., Crete M., Huot J., Maltais J. and Ouellet J.P. (1998) Food choice by white-tailed deer in relation to protein and energy content of the diet: a field experiment. *Oecologia*, **115**, 84–92.

Cortes C., Damasceno J.C., Jamot J. and Prache S. (2006) Ewes increase their intake when offered a choice of herbage species at pasture. *Animal Science*, **82**, 183–191.

Davies D.A., Fothergill H. and Morgan C.T. (1992) Assessment of contrasting perennial ryegrasses, with and without clover, under continuous sheep stocking in the uplands. 4. Animal performance in years 4-6. *Grass and Forage Science*, **47**, 3–249.

Dove H. and Milne J.A. (1994) Digesta flow and rumen microbial protein production in ewes grazing perennial ryegrass. *Australian Journal of Agricultural Research*, **45**, 1229–1245.

Fisher D.S., Mayland H.F. and Burns J.C. (1999) Variation in ruminants' preference for tall fescue hays cut either at sun-down or at sun-up. *Journal of Animal Science*, **77**, 762–768.

Forbes J.M. and Kyriazakis I. (1995) Food preferences in farm animals: why don't they always choose wisely? *Proceedings of the Nutrition Society*, **54**, 429–440.

Freddi A.J., Arzadún M., Sánchez E. and Di Salvo H. (2001) Production and quality of annual winter grasses in three environments. *Revista Argentina de Producción Animal*, **21**, 158–159.

Ganskopp D. (1995) Free-ranging angora goats: left- or right-handed tendency while grazing? *Applied Animal Behaviour Science*, **43**, 141–146.

Gibb M.J. and Treacher T.T. (1984) The performance of weaned lambs offered diets containing different proportions of fresh perennial ryegrass and white clover. *Animal Production*, **39**, 412–420.

Ginane C., Baumont R., Lassalas J. and Petit M. (2002) Feeding behaviour and intake of heifers fed on hays of various quality, offered alone or in a choice situation. *Animal Research*, **51**, 177–188.

Goering H.K. and Van Soest P.J. (1970) *Forage fiber analyses (apparatus, reagents, procedures and some applications), Agricultural Handbook 379*. Washington, DC: ARS-USDA.

Hirata M., Sakou A., Terayama Y., Furuya M. and Nanba T. (2008) Selection of feeding areas by cattle in a spatially heterogeneous environment: selection between two tropical grasses. *Journal of Ethology*, **26**, 327–338.

Hosoi E., Rittenhouse L.R., Swift D.M. and Richards R.W. (1995) Foraging strategies of cattle in a Y-maze: influence of food availability. *Applied Animal Behaviour Science*, **43**, 189–196.

Hou X.Z. (1991) *Diet selection in sheep*. PhD Thesis, Edinburgh: University of Edinburgh.

Hou X.Z., Lawrence A.B., Illius A.W., Anderson D. and Oldham J.D. (1991) Operant studies on feed selection in sheep. *Proceedings of the Nutrition Society*, **50**, 95A.

Illius A.W. and Gordon I.J. (1990) Constraints on diet selection and foraging behaviour in mammalian herbivores. In: Hughes R.N. (ed.) *Behavioural mechanisms of food selection*, pp. 369–392. New York, USA: Springer-Verlag.

Illius A.W., Gordon I.J., Elston D.A. and Milne J.D. (1999) Diet selection in goats: a test of intake-rate maximization. *Ecology*, **80**, 1008–1018.

James S.M., Kyriazakis I. and Emmans G.C. (2001) Diet selection of sheep: effects of adding urea to foods with different protein contents. *Animal Science*, **73**, 183–195.

Kyriazakis I. and Oldham J.D. (1997) Food intake and diet selection of sheep: the effect of manipulating the rates of digestion of carbohydrates and protein of the foods offered as a choice. *British Journal of Nutrition*, **77**, 243–254.

Littell R.C., Henry P.R. and Ammerman C.B. (1998) Statistical analysis of repeated measures data using SAS procedures. *Journal of Animal Science*, **76**, 1216–1231.

Moorby J.M., Evans R.T., Scollan N.D., MacRae J.C. and Theodorou M.K. (2006) Increased concentration of water-soluble carbohydrates in perennial ryegrass (*Lolium perenne* L.). Evaluation in dairy cows in early lactation. *Grass and Forage Science*, **61**, 52–59.

Newman J.A., Parsons A.J. and Harvey A. (1992) Not all sheep prefer clover: diet selection revisited. *Journal of Agricultural Science, Cambridge*, **119**, 275–283.

Newman J.A., Penning P.D., Parsons A.J., Harvey A. and Orr R.J. (1994) Fasting affects intake behaviour and diet preference of grazing sheep. *Animal Behaviour*, **47**, 185–193.

O'Reagain P.J. and Schwartz J. (1995) Dietary selection and foraging strategies of animals on rangeland: coping with spatial and temporal variability. In: Journet M., Grenet E., Demarquilly C., Farce M.H. and Theriez M. (eds) *Recent developments in the nutrition of herbivores*, pp. 407–423. Paris, France: INRA.

Parsons A.J., Newman J.A., Penning P.D., Harvey A. and Orr R.J. (1994) Diet preference of sheep: effects of recent diet, physiological state and species abundance. *Journal of Animal Ecology*, **63**, 465–478.

Prache S., Bechet G. and Damasceno J.C. (2006) Diet choice in grazing sheep: a new approach to investigate the relationships between preferences and intake rate on a daily time scale. *Applied Animal Behaviour Science*, **99**, 253–270.

Provenza F.D. (1995) Post-ingestive feedback as an elementary determinant of food preference and intake in ruminants. *Journal of Range Management*, **48**, 2–17.

Provenza F.D. (1996) Acquired aversions as the basis for varied diets of ruminant foraging rangelands. *Journal of Animal Science*, **74**, 2010–2020.

Provenza F.D., Villalba J.J., Dziba L.E., Atwood S.B. and Banner R.E. (2003) Linking herbivore experience, varied diets and plant biochemical diversity. *Small Ruminant Research*, **49**, 257–274.

Russell J.B., O'Connor J.D., Fox D.G., Van Soest P.J. and Sniffen C.J. (1992) A net carbohydrate and protein system for evaluating cattle diets: I. Ruminal fermentation. *Journal of Animal Science*, **70**, 3551–3561.

Rutter S.M. (2006) Diet preference for grass and legumes in free-ranging domestic sheep and cattle: current theory and future application. *Applied Animal Behaviour Science*, **97**, 17–35.

Rutter S.M., Orr R.J. and Rook A.J. (2000) Dietary preference for grass and white clover in sheep and cattle: an overview. In: Rook A.J. and Penning P.D. (eds) *Grazing management: the principles and practice of grazing, for profit and environmental gain, within temperate grassland systems*, BGS Occasional Symposium No. 34, pp. 73–78. Reading: British Grassland Society.

SAS (2000) *SAS/STAT User's Guide*. Version 8. Cary, NC: SAS Institute Inc.

Scott L.L. and Provenza F.D. (1999) Variation in food selection among lambs: effects of basal diet and foods offered in a meal. *Journal of Animal Science*, **77**, 2391–2397.

Simpson S.J., Sibly R.M., Lee K.P., Behmer S.T. and Raubenheimer D. (2004) Optimal foraging when regulating intake of multiple nutrients. *Animal Behaviour*, **68**, 1299–1311.

Stephens D.W. and Krebs J.R. (1986) *Foraging theory*. Princeton, USA: Princeton University Press.

Wales W.J., Kolver E.S., Thorne P.L. and Egan A.R. (2004) Diurnal variation in ruminal pH on the digestibility of highly digestible perennial ryegrass during continuous culture fermentation. *Journal of Dairy Science*, **87**, 1864–1871.

Westoby M. (1978) What are the biological bases of varied diets? *American Naturalist*, **112**, 627–631.