APPENDIX 1A.3

GRAZING BEHAVIOUR

M D Fraser

Plant, Animal and Microbial Science Department, Institute of Grassland and Environmental Research, Plas Gogerddan, Aberystwyth, Ceredigion, SY23 3EB, UK

GRAZING BEHAVIOUR

For a grazing animal there are few situations where there are not qualitative or quantitative limitations on the food items available for consumption (Hodgson, 1982). Consequently its intake is likely to be constrained by either digestive capacity; i.e. the product of the volume of the organ(s) used for the breakdown of plant tissue, and the digestive turnover within the organ(s) (Belovsky, 1986); or feeding time (Bunnell and Gillingham, 1985). By modifying aspects of its ingestive behaviour an animal can counteract these constraints and increase the probability of meeting its nutrient requirements from the available vegetation. However, feeding must be integrated with additional tasks necessary for survival and reproduction. Consequently time and energy may need to be partitioned between a number of activities. The approach generally applied to the study of feeding strategies, optimal foraging theory, assumes that animals maximise some objective function, usually energy captured per unit time, by choosing among alternate behaviours subject to a set of constraints (Stephens and Krebs, 1986).

Body size has a fundamental effect on the foraging strategy of an animal since this and related variables determine the overall time-energy constraints within food must be secured. In particular there is a strong relationship between body size and metabolic requirement. In general the food requirements of mammals increase with increasing body weight as a result of increasing costs of maintenance and production, although crucially this increase is not linear (Demment and Van Soest, 1985). Consequently, a larger ruminant requiring a greater absolute quantity of nutrients during a day will have less time per unit of nutrient to spend selectively foraging than does a smaller ruminant with a lower absolute requirement (Bell, 1970; Jarman, 1974), and large ungulates have been found to abandon selective grazing under conditions where it is still profitable for small ungulates to continue selective grazing (Schwartz and Ellis, 1981). Likewise, larger animals may be forced to move to taller, more accessible parts of the sward or graze other communities once preferred areas have been grazed too short to allow intakes to be maintained (Clutton-Brock *et al.*, 1987; Illius and Gordon, 1987). However, since the larger animal has a lower relative requirement it can in general meet its nutritional needs with relatively lower quality forage (Illius and Gordon, 1991). In addition, increasing body size should theoretically produce higher digestibilities because of longer retention times (Van Soest, 1982). Mouth size is highly correlated with body size, and again has a strong influence on the diet consumed. Small ungulates tend to have mouths adapted for carefully selecting discrete high quality food items while large species have mouths adapted for rapid ingestion of large quantities of undifferentiated items, often of comparatively low quality (Jarman and Sinclair, 1979). More specifically the dimensions of the incisor arcade determines the extent to which an animal can prehend and ingest discreet food items from within the spatial array of vegetation (Gordon and Illius, 1988; Flores *et al.*, 1989), and consequently determines the degree of selectivity that is mechanically possible for the forager to exhibit, and the time and energy costs of selectively foraging on specific plant parts or individuals.

Selection of dietary components can be thought of as occurring at a number of hierarchical levels (Jarman and Sinclair, 1979; Senft *et al.*, 1987). Firstly, in a given feeding bout an animal can choose a vegetation type or community on which to feed. This decision may be influenced by factors such as climate, topography and the availability of shelter (Arnold, 1984; Stuth, 1991) in addition to forage quality and quantity. Secondly, within a vegetation type or community an animal can choose among plant types or species to eat. Thirdly, it may choose which morphological units of those plants to eat. Depending on the choices made by a given animal, the composition of the diet selected may be substantially different to the proportions of various species or plant parts present within a particular community or sward (Arnold, 1960; Grant *et al.*, 1985; Grant *et al.*, 1987; Fraser and Gordon, 1997). Such selection minimises the adverse effects of pronounced seasonality in the quality and quantity of the food available for selection (Milne, 1974; Jarman and Sinclair, 1979; Grant and Hodgson, 1986). The scope for selection will depend on the heterogeneity of the vegetation the animal is feeding from and the spatial distribution of different plant components, and for domesticated species this is generally dictated by management regimes imposed by man.

The sown swards typical of intensive production systems are generally characterised by being highly digestible and consumption is more likely to be limited by quantity than quality of vegetation available (Hodgson *et al.*, 1991). In comparison indigenous plant communities are rarely limiting in overall vegetation quantity. However, such swards are generally characterised by a wide diversity of plant species which may offer extremes in digestibility (Grant and Campbell, 1978; Armstrong *et al.*, 1986). These differences in digestibility, the spatial distribution of particular plant species (Spalinger *et al.*, 1988) and seasonality of plant growth (Arnold *et al.*, 1966) can all be limiting to nutrient intake and result in the uneven distribution of grazing pressure both within and between plant communities (Hunter, 1962; Jarman and Sinclair, 1979; Grant and Maxwell, 1988). In such circumstances, utilisation of a given species, such as *Calluna*, may be dependent on the availability of another, more preferred species (Milne *et al.*, 1979; Vulink and Drost, 1991). If the density of a preferred species is too low or it is too widely dispersed then although it will be consumed if encountered, there may be no benefit to the animal in searching for it.

Despite growing interest in the environmental benefits of grazing (Hayes and Holl, 2003; Rook *et al.*, 2004; Pykala, 2005), and its potential role in promoting biodiversity within upland semi-natural communities (Grant *et al.*, 1963; Grant *et al.*, 1996a; Todd *et al.*, 2000; Marrs *et al.*, 2004), comparatively little data has been collected comparing the foraging behaviour of cattle and sheep in such environments, and the associated animal performance that can be achieved. Instead the focus has been on comparative resource use by domestic and wild herbivores; i.e. sheep and deer respectively (Milne *et al.*, 1978; Milne, 1980; Clarke *et al.*, 1995a; Clarke *et al.*, 1995b; Hester *et al.*, 1996; Hester and Baillie, 1998; Hester *et al.*, 1999) The limited number of studies with cattle and sheep have demonstrated that cattle are generally less selective grazers than sheep, and are prepared to consume significant quantities of invasive grasses such as *Nardus stricta* and *Molinia caerulea* (Grant *et al.*, 1985). When grazing *Calluna* moor, both animal species were found to preferentially graze *Vaccinium* spp., *Juncus* spp., grasses and *Carex* spp. (Grant *et al.*, 1987). However, the distribution of these species appeared to have a greater impact on the ability of the cattle to graze selectively. The sheep were also more selective than cattle when grazing *Calluna vulgaris* itself, and removed leafier shoot tips, while cattle removed more woody material. Thus cattle would be expected to have a greater impact on individual *Calluna vulgaris* plants than sheep, and by removing more of the shoot length they increase the risk of shoot death and the incidence of broken or uprooted shoots. However, there was also evidence that cattle are more reluctant than sheep to graze *Calluna vulgaris*, since their intakes were reduced proportionately more compared with their average intakes on hill grasslands (Hodgson and Eadie, 1986). Thus careful targeting of cattle grazing on *Calluna* heath is likely to be required if productivity and welfare are not to be compromised.

While differences between animal species in grazing behaviour and diet selection when grazing hill and upland communities have been documented (Grant *et al.*, 1985; Grant *et al.*, 1996b; Hester *et al.*, 1996; Fraser and Gordon, 1997; Hester *et al.*, 1999), very little robust data are currently available regarding differences between breeds in grazing behaviour, or on the impact of such differences on animal performance. Body size and associated allometric relationships with food intake, digestibility and selectivity could theoretically lead to differences in breed performance (Illius and Gordon, 1987; Illius, 1989). Research on suckler cows suggests that there are important differences in the way in which breeds of beef cow and their suckling calves perform in different nutritional environments (Wright *et al.*, 1994; Lowman *et al.*, 1996; Sinclair *et al.*, 1998) and it is possible that similar interactions exist in growing cattle. It is feasible that the poorer nutritional environments in the hills and uplands, resulting from a shorter growing season and lower herbage growth rates, may penalise large continental breeds with high nutrient requirements more than traditional, slower growing breeds.

Several studies of domestic and semi-domestic ruminants grazing *Calluna* heath have identified a seasonal shift in utilisation of heather in response to changes in grass quality (Colquhuon, 1970; Grant *et al.*, 1976; Bullock, 1985; Grant *et al.*, 1987; Fraser and Gordon, 1997). In general the pattern of use of heaths, i.e. mainly outside the growing season, reflects periods of shortage of the preferred components. Likewise, studies investigating grazing behaviour of hill sheep on heather and associated areas of sown grass or *Agrostis/Festuca* have established that amount of grass, in terms of height (cm) and weight (kg DM/ha), is a major determinant of the utilisation of heather (Grant and Hodgson, 1986). More recently it has been demonstrated reductions in stocking rate and associated increases in sward biomass can lead to a reduction in utilisation of heather (Hulme *et al.*, 2002; Pakeman *et al.*, 2003). The spatial distribution of the sward components also has an important role to play in influencing foraging behaviour (Clarke *et al.*, 1995a), with utilisation of heather declining rapidly with distance from grass (Hester and Baillie, 1998)

The low intake, digestibility and nutritional value of *Calluna vulgaris* has been demonstrated in detailed feeding studies that suggested that only the shoots of the current season harvested in July provided sufficient intake of digestible organic matter to maintain the live weight of sheep (Milne, 1974). In addition, *Calluna vulgaris* contains significant amounts of tannins (Jalal *et al.*, 1982). These are polyphenolic secondary compounds that can react by hydrogen-bonding with plant protein in the near neutral pH range to form condensed tannin-protein complexes which are insoluble at pHs found in the rumen, but dissociate below pH 3-5. It is now recognised that the nutritional role of condensed tannins for ruminants depends on their concentration, structure and molecular weight in plants. High levels may depress intake and the digestion of protein and fibre (Murray *et al.*, 1981), and consequently tannin phenolics have been recognised as one of the factors affecting intake and diet selection by ruminants (Robbins *et al.*, 1987; McArthur *et al.*, 1993). At the same time tannins within grazed forages have been shown to be instrumental in reducing internal parasite burdens (Niezen *et al.*, 1996; Niezen *et al.*, 1998), and recent experimental work has found that goats grazing on improved pasture and supplemented with *Calluna vulgaris* have lower faecal egg counts (Osoro *et al.*, 2007).

REFERENCES

ARMSTRONG R.H., COMMON T.G. and SMITH H.K. (1986) The voluntary intake and *in vivo* digestibility of herbage harvested from indigenous hill plant communities. *Grass and Forage Science,* **41**, 53-60.

ARNOLD G.W. (1960) The effect of the quantity and quality of pasture available to sheep on their grazing behaviour. *Australian Journal of Agricultural Research,* **11**, 1026-1033.

ARNOLD G.W. (1984) Comparison of the time budgets and circadian patterns of maintenance activities in sheep, cattle and horses grouped together. *Applied Animal Behaviour Science,* **13**, 19-30.

ARNOLD G.W., BALL J., MCMANUS W.R. and BUSH I.R. (1966) Studies on the diet of the grazing animal. I Seasonal changes in the diet of sheep grazing on pastures of different availability and composition. *Australian Journal of Agricultural Research,* **17**, 543-556.

BELL R.H.V. (1970) The use of the herb layer by grazing ungulates in the Serengeti. In: Watson A. (ed). *Animal Populations in Relation to their Food Resources*. pp. 111-123. Oxford: Blackwell Scientific Publications.

BELOVSKY G.E. (1986) Generalist herbivore foraging and its role in competitive interactions. *American Zoologist,* **26**, 51-69.

BULLOCK D.J. (1985) Annual diets of hill sheep and feral goats in southern Scotland. *Journal of Applied Ecology,* **22**, 423-433.

BUNNELL F.L. and GILLINGHAM M.P. (1985) Foraging behavior: Dynamics of dining out. In: Hudson R.J. and White R.G. (eds). *Bioenergetics of Wild Herbivores*. pp. 53-79. Boca Raton, Florida: CRC Press.

CLARKE J.L., WELCH D. and GORDON I.J. (1995a) The influence of vegetation pattern on the grazing of heather moorland by red deer and sheep .1. The location of animals on grass heather mosaics. *Journal of Applied Ecology,* **32**, 166-176.

CLARKE J.L., WELCH D. and GORDON I.J. (1995b) The influence of vegetation pattern on the grazing of heather moorland by red deer and sheep .2. The impact on heather. *J Appl Ecol ER -,* **32**, 177-186.

CLUTTON-BROCK T.H., IASON G.R. and GUINNESS F.E. (1987) Sexual segregation and density-related changes in habitat use in male and female red deer (*Cervus elaphus*). *Journal Of Zoology,* **211**, 275-289.

COLQUHUON I.R. (1970) *The Grazing Ecology of Red Deer and Blackface Sheep in Perthshire, Scotland*. The Grazing Ecology of Red Deer and Blackface Sheep in Perthshire, Scotland. Edinburgh: University of Edinburgh.

DEMMENT M.W. and VAN SOEST P.J. (1985) A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *American Naturalist,* **125**, 641-675.

FLORES E.R., PROVENZA F.D. and BALPH D.F. (1989) The effect of experience on the foraging skill of lambs: Importance of plant form. *Applied Animal Behaviour Science,* **23**, 285-291.

FRASER M.D. and GORDON I.J. (1997) The diet of goats, red deer and South American camelids feeding on three contrasting Scottish upland vegetation communities. *Journal of Applied Ecology,* **34**, 668-686.

GORDON I.J. and ILLIUS A.W. (1988) Incisor arcade structure and diet selection in ruminants. *Functional Ecology,* **2**, 15-22.

GRANT S.A. and CAMPBELL D.R. (1978) Seasonal variation in *in vitro* digestibility and structural carbohydrate content of some commonly grazed plants of blanket bog. *Journal of the British Grassland Society,* **33**, 167-173.

GRANT S.A. and HODGSON J. (1986) Grazing effects on species balance and herbage production in indigenous plant communities. In: Gudmundsson O. (ed). *Grazing Research at Northern Latitudes*. pp. 69-77. London: Plenum Publishing Corportation.

GRANT S.A., HUNTER R.F. and CROSS C. (1963) The effects of muirburning *Molinia*-dominant communities. *Journal of the British Grassland Society,* **18**, 249-257.

GRANT S.A., LAMB W.I.C., KERR C.D. and BOLTON G.R. (1976) The utilization of blanket bog vegetation by grazing sheep. *Journal of Applied Ecology,* **13**, 857-869.

GRANT S.A. and MAXWELL T.J. (1988) Hill vegetation and grazing animals: the biology and definition of management options. In: Usher M.B. and Thompson D.B.A. (eds). *Ecological Change in the Uplands*. pp. 201-214. Oxford: Blackwell Scientific Publications.

GRANT S.A., SUCKLING D.E., SMITH H.K., TORVELL L.F. and HODGSON J. (1985) Comparative studies of diet selection by sheep and cattle grazing individual hill plant communities as influenced by season of the year. 1. The indigenous grasslands. *Journal of Ecology,* **73**, 987-1004.

GRANT S.A., TORVELL L., COMMON T.G., SIM E.M. and SMALL J.L. (1996a) Controlled grazing studies on *Molinia* grassland: Effects of different seasonal patterns and levels of defoliation on *Molinia* growth and responses of swards to controlled grazing by cattle. *Journal of Applied Ecology,* **33**, 1267-1280.

GRANT S.A., TORVELL L., SIM E.M., SMALL J.L. and ARMSTRONG R.H. (1996b) Controlled grazing studies on *Nardus* grassland: Effects of between-tussock sward height and species of grazer on *Nardus* utilization and floristic composition in two fields in Scotland. *Journal of Applied Ecology,* **33**, 1053-1064.

GRANT S.A., TORVELL L., SMITH H.K., SUCKLING D.E. and HODGSON J. (1987) Comparative studies of diet selection by sheep and cattle: blanket bog and heather moor. *Journal of Ecology,* **75**, 947-960.

HAYES G.F. and HOLL K.D. (2003) Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology,* **17**, 1694-1702.

HESTER A.J. and BAILLIE G.J. (1998) Spatial and temporal patterns of heather use by sheep and red deer within natural heather/grass mosaics. *Journal of Applied Ecology,* **35**, 772-784.

HESTER A.J., GORDON I.J., BAILLIE G.J. and TAPPIN E. (1999) Foraging behaviour of sheep and red deer within natural heather grass mosaics. *Journal of Applied Ecology,* **36**, 133-146.

HESTER A.J., MITCHELL F.J.G., GORDON I.J. and BAILLIE G.J. (1996) Activity patterns and resource use by sheep and red deer grazing across a grass/heather boundary. *Journal Of Zoology,* **240**, 609-620.

HODGSON J. (1982) Influence of sward characteristics on diet selection and herbage intake by the grazing animal. In: Hacker J.B. (ed). *Nutritional Limits to Animal Production from Pastures*.

HODGSON J. and EADIE J. (1986) Vegetation resources and animal nutrition in hill areas: agricultural and environmental implications. In: O'Toole M. (ed). *Hill Farming Symposium, Galaway 1984*. pp. 118-133. Dublin: An Foras Taluntais.

HODGSON J., FORBES T.D.A., ARMSTRONG R.H., BEATTIE M.M. and HUNTER E.A. (1991) Comparative studies of the ingestive behaviour and herbage intake of sheep and cattle grazing indigenous hill plant communities. *Journal of Applied Ecology,* **28**, 205-227.

HULME P.D., MERRELL B.G., TORVELL L., FISHER J.M., SMALL J.L. and PAKEMAN R.J. (2002) Rehabilitation of degraded *Calluna vulgaris* (L.) Hull-dominated wet heath by controlled sheep grazing. *Biological Conservation,* **107**, 351-363.

HUNTER R.F. (1962) Hill sheep and their pasture: a study of sheep-grazing in south east Scotland. *Journal of Ecology,* **50**, 651-680.

ILLIUS A.W. (1989) Allometry of food intake and grazing behaviour with body size in cattle. *Journal of Agricultural Science,Cambridge,* **113**, 259-266.

ILLIUS A.W. and GORDON I.J. (1987) The allometry of food intake in grazing ruminants. *Journal of Animal Ecology,* **56**, 989-999.

ILLIUS A.W. and GORDON I.J. (1991) Prediction of intake and digestion in ruminants by a model of rumen kinetics integrating animal size and plant characteristics. *Journal of Agricultural Science,Cambridge,* **116**, 145-157.

JALAL M.A.F., READ D.J. and HASLAM E. (1982) Phenolic composition and its seasonal variation in Calluna vulgaris. *Phytochemistry,* **21**, 1397-1401.

JARMAN P.J. (1974) The social organisation of antelope in relation to their ecology. *Behaviour,* **48**, 215-267.

JARMAN P.J. and SINCLAIR A.R.E. (1979) Feeding strategy and the pattern of resource partitioning in ungulates. In: Sinclair A.R.E. and Norton-Griffiths M. (eds). *Serengeti, Dynamics of an Ecosystem*. pp. 130-163. Chicago: University of Chicago Press.

LOWMAN B.G., HINKS C.E., HUNTER E.A. and SCOTT N.A. (1996) Effect of breed type, sex, method of rearing and winter nutrition on lifetime performance and carcass composition in a 20-month beef system: Grazing performance. *Animal Science,* **63**, 215-222.

MARRS R.H., PHILLIPS J.D.P., TODD P.A., GHORBANI J. and LE DUC M.G. (2004) Control of *Molinia caerulea* on upland moors. *Journal of Applied Ecology,* **41**, 398-411.

MCARTHUR C., ROBBINS C.T., HAGERMAN A.E. and HANLEY T.A. (1993) Diet selection by a ruminant generalist browser in relation to plant chemistry. *Canadian Journal of Zoology,* **71**, 2236-2243.

MILNE J.A. (1974) The effects of season and age of stand on the nutritive value of heather (*Calluna vulgaris*, L. Hull) to sheep. *Journal of Agricultural Science,Cambridge,* **83**, 281-288.

MILNE J.A. (1980) Comparative digestive physiology and metabolism of the red deer and the sheep. *Proceedings of the New Zealand Society of Animal Production,* **40**, 151-157.

MILNE J.A., BAGLEY L. and GRANT S.A. (1979) Effects of season and level of grazing on the utilization of heather by sheep. 2. Diet selection and intake. *Grass and Forage Science,* **34**, 45-53.

MILNE J.A., MACRAE J.C., SPENCE A. and WILSON S. (1978) A comparison of the voluntary intake and digestion of forages at different times of the year by the sheep and red deer (*Cervus elaphus*). *British Journal of Nutrition,* **40**, 347-357.

MURRAY M.G., LEWIS A.R. and COETZEE A.M. (1981) An evaluation of capture techniques for research on impala populations. *South African Journal of Wildlife Research,* **11**, 105-109.

NIEZEN J.H., CHARLESTON W.A.G., HODGSON J., MACKAY A.D. and LEATHWICK D.M. (1996) Controlling internal parasites in grazing ruminants without recourse to anthelmintics - approaches, experiences and prospects. *International Journal for Parasitology,* **26**, 983-992.

NIEZEN J.H., ROBERTSON H.A., WAGHORN G.C. and CHARLESTON W.A.G. (1998) Production, faecal egg counts and worm burdens of ewe lambs which grazed six contrasting forages. *Veterinary Parasitology,* **80**, 15-27.

OSORO K., BENITO-PENA A., FRUTOS P., GARCIA U., ORTEGA-MORA L.M., CELAYA R. and FERRE I. (2007) The effect of heather supplementation on gastrointestinal nematode infections and performance in Cashmere and local Celtiberic goats on pasture. *Small Ruminant Research,* **67**, 184-191.

PAKEMAN R.J., HULME P.D., TORVELL L. and FISHER J.M. (2003) Rehabilitation of degraded dry heather *Calluna vulgaris* (L.) Hull moorland by controlled sheep grazing. *Biological Conservation,* **114**, 389-400.

PYKALA J. (2005) Plant species responses to cattle grazing in mesic semi-natural grassland. *Agriculture Ecosystems & Environment,* **108**, 109-117.

ROBBINS C.T., HANLEY T.A., HAGERMAN A.E., HJELJORD O., BAKER D.L., SCHWARTZ C.C. and MAUTZ W.W. (1987) Role of tannins in defending plants against ruminants: reduction in protein availability. *Ecology,* **68**, 98-107.

ROOK A.J., DUMONT B., ISSELSTEIN J., OSORO K., WALLISDEVRIES M.F., PARENTE G. and MILLS J. (2004) Matching type of livestock to desired biodiversity outcomes in pastures - a review. *Biological Conservation,* **119**, 137-150.

SCHWARTZ C.C. and ELLIS J.E. (1981) Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. *Journal of Applied Ecology,* **18**, 343-353.

SENFT R.L., COUGHENOUR M.B., BAILEY D.W., RITTENHOUSE L.R., SALA O.E. and SWIFT D.M. (1987) Large herbivore foraging and ecological hierarchies. *Bioscience,* **37**, 789-799.

SINCLAIR K.D., YILDIZ S., QUINTANS G. and BROADBENT P.J. (1998) Annual energy intake and the performance of beef cows differing in body size and milk potential. *Animal Science,* **66**, 643-655.

SPALINGER D.E., HANLEY T.A. and ROBBINS C.T. (1988) Analysis of the functional response in foraging in the Sitka black-tailed deer. *Ecology,* **69**, 1166-1175.

STEPHENS D.W. and KREBS J. (1986) The economics of choice: trade-offs and herbivory. *Foraging Theory*. pp. 104-127. Princeton University Press: New Jersey.

STUTH J.W. (1991) Foraging behavior. In: Heitschmidt R.K. and Stuth J.W. (eds). *Grazing management. An ecological perspective*. pp. 65-83. Portland, Oregon: Timber Press.

TODD P.A., PHILLIPS J.D.P., PUTWAIN P.D. and MARRS R.H. (2000) Control of *Molinia caerulea* on moorland. *Grass and Forage Science,* **55**, 181-191.

VAN SOEST P.J. (1982) The Nutritional Ecology of the Ruminant. Oregon: O & B Books.

VULINK J.T. and DROST H.J. (1991) A causal analysis of diet composition in free ranging cattle in reed-dominated vegetation. *Oecologia,* **88**, 167-171.

WRIGHT I.A., JONES J.R., MAXWELL T.J., RUSSEL A.J.F. and HUNTER E.A. (1994) The effect of genotype X environment interactions on biological efficiency in beef-cows. *Animal Production,* **58**, 197-207.