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Comparative abilities of different herbivorous species to graze in upland areas: consequences for productivity and vegetation *

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Summary — Animal size, as it influences digestive function and ingestive behaviour, is the most important factor influencing animal production and vegetation change. A review of the evidence suggests that sheep are more adapted to grazing semi-natural vegetation than cattle. Because of the differences between sheep and cattle in their grazing style on heterogeneous pastures, the combined use of the 2 species can lead to the achievement of improved production and pasture management objectives.

grazing behaviour / cattle sheep / upland areas / productivity

Résumé — Aptitude comparée de différentes espèces herbivores à pâturer dans des zones d'altitude : conséquences sur la productivité des animaux et sur la végétation. *Le format des animaux est la variable qui influence le plus la productivité des troupeaux et l'utilisation des pâturages. Les besoins alimentaires, la capacité à digérer les fourrages et l'incapacité à trier les aliments augmentent avec le format. Les résultats expérimentaux suggèrent que les ovins sont mieux adaptés au pâturage de la végétation semi-naturelle que les bovins. À cause des différences entre les ovins et les bovins dans la façon de pâturer la végétation hétérogène, l'association des deux espèces peut permettre d'améliorer non seulement la productivité des animaux mais encore la gestion des pâturages.*

comportement au pâturage / bovins / ovins / zone de montagne / productivité

The species of domesticated animals that graze the semi-natural vegetation communities in the upland areas of Europe are a result of a series of economic and social pressures which have been exerted over several centuries. Although these species have attributes which have allowed them to become adapted to such environments, in many cases it has been the value of their products, either as a source of food

* Communication to the 7th Conference on nutrition and feeding of herbivores, Paris, 25-26 March 1992. See *Ann Zootech* 42, 115.

for those living in upland areas or as salable products, such as meat, milk, cheese or wool, that has determined which species have grazed in particular environments. Neither the degree to which animals are adapted to particular environments nor the impact that these species have had upon the vegetation have been major determinants of which species graze these potentially fragile resources. In the future with the need to manage these resources to meet a wider range of objectives, which will include environmental as well as socio-economic considerations, there is an opportunity to match more effectively the species of animals utilising these upland areas to meet these new objectives. Our knowledge of the animal factors, which influence feeding behaviour, diet selection and intake and which, in turn, influence animal productivity and impact on vegetation, is increasing rapidly. However, there is still much research that needs to be undertaken before one can adequately predict the consequences of grazing by different species on what are complex resources differing spatially in species composition, structure and digestibility. The current state of knowledge is described in this paper.

ATTRIBUTES OF DIFFERENT SPECIES

There are a number of animal variables that are important determinants of grazing behaviour of ruminants, which is the subset of herbivores that will be mainly discussed. The most all-pervasive variable is body size. Absolute feed requirements, the capacity to digest food of lower quality, and the inability of fine-grained food selection all increase with body weight (Gordon and Illius, 1988; Illius and Gordon, 1987; Demment and Van Soest, 1985). As well as being influenced by body size, which determines the size of the mouth, the ability for fine-grained food selection from heterogeneous plant material, for example, by the goat, is associated with a narrower and more pointed mouth whilst a broad and flat muzzle, as in cattle, is associated with a low degree of selectivity (Gordon and Illius, 1988). In general terms, these attributes of body size and mouth dimensions, which influence diet selection, foraging strategy and digestive capability, are linked and have led to the classification of ruminants into grazers, browsers and mixed feeders. Cattle and sheep are considered as grazers, goats as predominantly browsers and deer as mixed grazers (Gordon and Iason, 1989).

Although such a classification has general applicability, there are considerable differences within a class, for example, between sheep and cattle, in grazing behaviour. In a large study on the ingestive behaviour of sheep and cattle grazing a range of semi-natural vegetation communities in Scotland throughout the year, *viz Agrostis-Festuca* species, *Nardus stricta*, *Molinia caerulea*, *Calluna vulgaris* and *Calluna/Eriophorum/Trichophorum* species, the responses in ingestive behaviour of sheep and cattle differed (Hodgson *et al,* 1991). Table I gives average data values across all these community types. Whilst bite rate was similar between species, the sheep grazed for longer than cattle, particularly in *Agrostis-Festuca*, *Nardus* and *Calluna* communities. However, the combination of bite rate and grazing time, *ie* total daily bites, was similar between species. Intake per bite was obviously higher for cattle than sheep but when expressed on a liveweight basis was higher for sheep then cattle. This difference between species in intake per bite was reflected in higher daily herbage intake per unit of liveweight by sheep. The digestibility of the diet selected, as described by *in vitro* digestibility determinations on oesophageal-fistulated extrusa samples, was also higher in sheep than cattle.

Table I. Effect of animal species on extrusa digestibility, herbage intake, bite rate, grazing time, daily bites, intake per bite and digestible organic matter intake when grazing a range of semi-natural vegetation (from Hodgson *et al,* 1991).

	Animal species		
	Cattle	*Sheep*	*SED*
Extrusa digestibility	0.616	0.660	0.078
Herbage organic matter intake (g OM kg $LW^{-1}day^{-1}$)	16.3	22.6	0.64
Bite rate (bite min^{-1})	50.5	49.0	1.38
Grazing time (min day^{-1})	563	574	15.9
Daily bites (x 10^{-3})	29.3	28.9	1.65
Intake per bite (mg OM kg $LW^{-1}bite^{-1}$)	0.57	0.85	0.052
Digestible organic matter intake (g DOM kg $LW^{-1}day^{-1}$)	11.0	15.7	0.52

SED = standard error of difference between means.

The longer grazing times of sheep, the greater depth of grazing, which reflects a less surface-orientated grazing style than cattle, and the higher digestibility of the diet, all indicate the greater selectivity by sheep than cattle. The differences were greatest in the shrub communities, *ie Calluna* and least on the grassy communities.

Variations in diet digestibility both within and between periods of measurements were also consistently greater for cattle than for sheep in the same study (Hodgson *et al,* 1991), but the reverse was the case for variations in biting rate and intake per bite. This evidence suggests that behavioural adjustments were directed primarily to the maintenance of dietary nutrient concentration in sheep and the maintenance of rate of intake in cattle, and is consistent with the generally greater degree of grazing selectivity exhibited by the sheep. These results support the general theory that strategies leading to maintenance of nutrient concentration in the diet are more important in small than in large ungulate species and indicate that body size effects apply to the exercise of choice between plant species and components within a single plant community.

The higher intake of sheep relative to cattle and in relation to the energy requirements of the 2 species suggest that sheep in many upland areas would have advantages over cattle in meeting nutrient demands. This can be seen from figure 1 which shows the digestible organic matter intakes of sheep and cattle on a range of plant communities (Hodgson *et al,* 1991). The dotted lines show the estimated requirements of sheep and cattle for mainte-

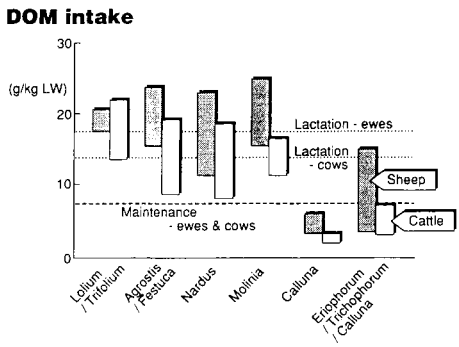

Fig 1. The annual range in digestible organic matter intakes by sheep and cattle obtained by grazing semi-natural vegetation communities in Scotland (after Armstrong and Hodgson, 1986).

nance of liveweight and for lactation. This basic set of information is essential for a wider understanding of the potential use of such species not only for grazing large areas of one community but also for more heterogeneous circumstances. Similar information is currently being obtained at the Macaulay Land Use Research Institute for red deer, goats and a South American Camelid species, the guanaco, to identify which species are most suited to grazing particular plant communities. Preliminary results on grazing behaviour suggest that all these species are as selective as sheep with deer selecting from the upper part of the sward. Guanacos were found to be particularly adept at selecting from shrub vegetation but were not particularly selective on grassy swards (Fraser, M and Gordon, I, personal communication).

The question arises as to the mechanisms that ruminants use in making decisions about where to select bites from within the plant community. A ruminant may take 10–40 000 bites per day and the ability to gain and process information is likely to be complex and the monitoring of individual bite choices difficult (Milne, 1991). Evidence from studies in which one or more of the special senses, sight, smell, touch or taste, have been impaired suggests that taste is the most likely sense to the involved (Krueger *et al,* 1974). The results in table II show the relative preference indices for 3 grasses by sheep which change to the greatest extent when taste is impaired. This finding is in agreement with other observations that sampling of vegetation, in other words, the taking of a small number of bites from different areas, has an important role to play in the diet selection process.

To date we have considered only discrete vegetation communities but in most semi-natural vegetation there is a range of plant communities and the choices made by herbivores can be potentially large. Optimal Foraging Theory would suggest that ruminants would attempt to maximise their

Table II. Relative preference indices for 3 grasses when sheep grazed summer range in the United States, the special senses being impaired independently (from Krueger *et al,* 1974).

	Alpine timothy (Phleum alpinum)	*Mountain brome* (Bromus marginatus)	*Onion grass* (Melica spectabilis)
Control	1.2	2.0	1.5
Sight impaired	1.8	2.4	2.0
Smell impaired	1.4	1.5	1.7
Touch impaired	1.4	2.4	1.9
Taste impaired	0.2	0.8	1.1

metabolisable energy (ME) intake whilst minimising their energy expenditure in obtaining that intake. Such a theory implies that animals will select a diet of high digestibility, provided that the costs of obtaining that high quality diet, either in terms of the mechanical strength required to obtain a bite or in terms of the time required to select a bite, do not become too high. Evidence to support such a theory is being obtained as part of several research efforts describing the foraging strategy of various ruminants. The earliest evidence under UK conditions relates to sheep behaviour when grazing a mixture of 3 vegetation communities, *Agrostis-Festuca* species, *Calluna vulgaris* and *Nardus stricta* (Hunter, 1962). Information on the sitings of sheep demonstrated that *Agrostis-Festuca*, which has a high digestibility, was preferred during most of the year except when its availability relative to *Calluna* declined. At low availabilities of biomass, the energy cost of obtaining additional ME intake appeared to decline and the net benefit would be greater from grazing *Calluna*, even though it has a lower digestibility. *Nardus*, although it has a high biomass, was not preferred presumably because of the toughness of its leaves and the energy cost associated with taking bites from *Nardus*. Information on the grazing behaviour of cattle, deer and goats in a study on the Island of Rhum, Scotland, can be interpreted in a similar manner (Gordon, 1989). The grazing behaviour of the red deer *(Cervus elaphus)* was in many ways similar to sheep, with both species having large incisor breadth relative to metabolic requirements, such that they grazed on grass swards of high nutrient density whilst they were available. Cattle with a large body size, longer digesta passage and smaller incisor breath: metabolic requirements also fed on high nutrient-dense grasses but appeared more prepared to eat grasses of lower nutrient density but not heath species. Goats grazed herbage with a high cell wall content either as grasses or heather and, interestingly, seemed to have a requirement for lignified fibrous feeds. These differences between species in site selection require further exploration.

The approach described previously is only applicable in similar areas to those studied since there was no control exerted over the biomass of different plant communities. What is required is a more systematic examination of the interaction between nutrient density and availability on site selection. Such an approach has been adopted with 0.25 *Agrostis-Festuca*/0.75 *Calluna* heather combinations where the grass biomass per unit area has been varied and the proportion of the lower nutritive value species, heather, in the diet of sheep examined (Milne and Grant, 1987). Sheep selected a diet that contained an increasing proportion of *Calluna* as the amount of biomass of *Agrostis-Festuca* declined. The study also showed that not only was the biomass of the *Agrostis-Festuca* important but that the rate of elongation of new leaves of *Agrostis-Festuca* also influenced the amount of *Calluna* that was ingested.

A further example that extends the approach to cattle is in *Nardus*-dominated vegetation communities. *Nardus* is found to be associated with intertussock *Agrostis-Festuca* species. By maintaining the biomass of the intertussock species over the summer at a range of biomasses, relationships between the proportion of *Nardus* in the diet and the biomass of the *Agrostis-Festuca* have been developed for both sheep and cattle (Grant and Hodgson, 1986). It can be seen (fig 2) that the relationships are different with the cows being more prepared than sheep to graze *Nardus* at any height or biomass of the intertussock species.

The differences between sheep and cattle in these relationships can be explained

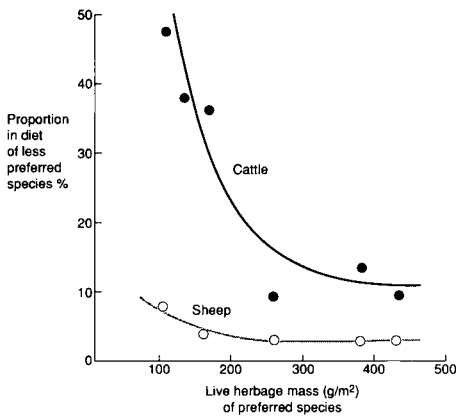

Fig 2. The relation between the biomass of the preferred species, *Agrostis-Festuca*, and the proportion of *Nardus* in the diet of sheep (–O–) and cattle (–●–) grazing *Nardus*-dominated vegetation (after Grant and Hodgson, 1986).

in terms of the different abilities of the species to be selective and thus maintain diet quality and by their ability to prehend and sever vegetation. One interesting point that arises is that the diet selected never becomes zero for any component. This can be explained in terms of the requirement of ruminant species to continue to sample vegetation, as discussed previously, when they are making choices between different plant communities. Although sight is considered to be important in determining the sites at which animals graze, taste, it is argued, also remains important and the sampling between different plant communities is a reflection of the need to reinforce information on community choice (Milne, 1991).

The experimental approach described above also has importance in considering complementarity of grazing between different species. If there is no complementarity, the relationship between proportion of *Nardus* in the diet and the biomass of the intertussock species should be intermediate provided that the same animal biomass is applied as 50:50 sheep/cattle. If the relationship changes, then complementarity can be deduced. In an experiment currently being conducted on a *Nardus*-dominated community, the performance of sheep when grazed at a range of intertussock sward heights alone or when grazed with cattle is being investigated. Results from the first year of the experiment (Howard C and Wright IA, personal communication) show clearly that complementarity can be achieved. It is likely that the combinations of animal species may not only lead to improvements in animal productivity but be essential if objectives in relation to the management of vegetation are to be achieved.

These experimental approaches on relatively simple combinations of vegetation types allow the development of our understanding of more complex vegetation mixes. This has made possible the development of a computer model to predict where sheep will graze on semi-natural vegetation in the upland areas of the UK and what the offtake will be for each vegetation type (Armstrong, 1991). The computer model contains a series of sub-models which, on a daily basis, allow: i) the biomass of the different vegetation types to change through growth, senescence and grazing; and ii) the grazing of the biomass produced according to a foraging model, which permits sheep to select from a range of communities in relation to quality and biomass. The model requires input of the different vegetation types, the region and altitude of the area and the numbers of sheep that graze that area in each month. The output of the model is currently the monthly offtake or proportion of utilisation for each vegetation type. A particular interest is in the offtake of *Calluna* which is under considerable pressure from overgrazing in some areas of Scotland. The model has

been expanded to include deer grazing since wild deer numbers have increased dramatically in the last 20 years and are a partial cause of overgrazing (Armstrong H, personal communication).

As our understanding increases, such models can become of wider use. For example, the distribution of vegetation communities in terms of their spatial distribution is not considered at present. Current research will allow such information to be included in the model with a Geographical Information System approach being used in conjunction with a rule-based foraging model to predict offtake of different species from heterogeneous areas.

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