Rook, A. J. and Tallowin, J. R. B. 2003. Grazing and pasture management for plant biodiversity benefit. *Animal Research.* 52 (2), pp. 181-189.

Grazing and pasture management for biodiversity benefit

Andrew Rook, Jeremy Tallowin

Anim. Res. 52 (2003) 181–189

DOI: 10.1051/animres:2003014

Review article

Grazing and pasture management for biodiversity benefit

Andrew J. ROOK*, Jeremy R.B. TALLOWIN

Soils, Environmental and Ecological Science Department, Institute of Grassland and Environmental Research, North Wyke, Okehampton, Devon EX20 2SB, UK

(Received 19 August 2002; accepted 25 February 2003)

Abstract — The primary role of grazing animals in grassland biodiversity management is maintenance and enhancement of sward structural heterogeneity, and thus botanical and faunal diversity, by selective defoliation due to dietary choices, treading, nutrient cycling and propagule dispersal. Most research on dietary choices uses model systems that require considerable extrapolation to more complex communities. Grazing animals' diets are constrained by temporal and spatial changes in sward structure, plant defence mechanisms, herbage availability, plant phenology and animal physiological state. Potentially, these could be exploited to manipulate choice in diverse communities. Dietary choice differs between animal species, driven by factors such as body size, digestive physiology and dental anatomy. There is anecdotal evidence for breed differences but little experimentation, with genetic effects often confounded with background experience. There is information about landscape-scale breed and background effects but little about parameters such as bite and feeding station areas that allow reconstruction of the development of small-scale sward patchiness. An experiment at five European sites is examining breed effects on grazing behaviour, structural, floral and faunal diversity, animal production and economic impacts. In another project, calves are being reared by their own mothers or by cows of another breed allowing genetic effects on grazing behaviour to be separated from effects of early experience. 'Designer animals' may be needed to deliver desired grazing behaviour and biodiversity outcomes, either by breeding or by the use of training and previous experience to manipulate choices. Application of research results requires consideration of conservation goals, whether at landscape, habitat, plant community or plant species level. There is a need to replace stocking rate prescriptions with sward-based methods and to integrate biodiversity goals into intensive systems. Major gaps in our knowledge of grazing behaviour and its impact on biodiversity remain, necessitating greater integration of plant ecophysiology, plant community ecology and animal behavioural ecology research.

grazing / biodiversity / pasture management / dietary choices / animal type

* Correspondence and reprints
Tel.: +44 1837 883548; fax: +44 1837 82139; e-mail: aj.rook@bbsrc.ac.uk

Résumé — Pâturage et gestion des prairies pour davantage de biodiversité. Le rôle majeur des animaux au pâturage dans la conservation de la biodiversité des prairies permanentes est de maintenir et de développer l'hétérogénéité du couvert végétal par la défoliation sélective, selon les choix alimentaires, par le piétinement, le recyclage des éléments nutritifs et la dispersion des graines. Ainsi le pâturage favorise la diversité floristique de la prairie et la diversité faunistique associée. La plupart des recherches sur les choix alimentaires utilisent des situations modèles qui exigent des extrapolations considérables pour des communautés végétales plus complexes. En effet, le régime alimentaire des animaux au pâturage dépend des changements spatio-temporels de la structure du couvert végétal, des mécanismes de défense des plantes, de la disponibilité en herbe, de la phénologie des plantes et de l'état physiologique des animaux. Potentiellement, ces facteurs peuvent être exploités pour orienter les choix alimentaires dans diverses communautés végétales. Les choix alimentaires diffèrent entre les espèces animales, selon des facteurs comme la taille de l'animal, la physiologie de la digestion et l'anatomie dentaire. Des différences entre races ont été mises en évidence sur la base d'une démarche plus empirique qu'expérimentale, les effets génétiques étant souvent confondus avec les effets de l'environnement et de l'expérience alimentaire des animaux. Il existe également des données sur l'effet de la race et du milieu dans lequel évolue l'animal à l'échelle large du paysage, mais peu au sujet de paramètres tels que la surface des bouchées et des stations alimentaires qui permettent la restauration de l'hétérogénéité du pâturage à une échelle plus petite. Un essai conduit actuellement sur cinq sites européens a pour but d'étudier l'influence de la race sur le comportement au pâturage, la diversité de la structure et de la flore de la prairie ainsi que celle de la faune associée, la production animale et l'impact économique. Dans une autre étude, des veaux sont élevés soit par leur mère soit par des vaches d'une autre race afin de séparer sur le comportement au pâturage les effets liés aux facteurs génétiques de ceux liés à l'apprentissage dans le jeune âge. En orientant les choix alimentaires des animaux, par la sélection génétique ou bien par l'expérience dans le jeune âge et l'apprentissage, on pourrait utiliser des animaux 'modèles' pour favoriser des comportements de pâturage désirés, et par voie de conséquence la biodiversité de la prairie. La mise en application des résultats de la recherche doit prendre en compte les objectifs de conservation des espaces pastoraux aussi bien à l'échelle du paysage, que de l'habitat, de la communauté ou de l'espèce végétale. Il devient alors fondamental de remplacer les méthodes traditionnelles de conduite du pâturage, faisant appel à la notion de chargement, par des méthodes basées sur l'état du couvert végétal, et aussi d'intégrer des objectifs de biodiversité dans les systèmes d'élevage intensif. De nombreuses lacunes dans notre connaissance du comportement de pâturage et de son impact sur la biodiversité demeurent. Il est nécessaire de mieux intégrer les recherches menées en écophysiologie des plantes, en écologie des communautés végétales et écologie comportementale des animaux.

pâturage / biodiversité / conduite de la prairie / choix alimentaires / type d'animal

1. INTRODUCTION

In this paper, we review the role of the grazing animal in the management of grasslands for biodiversity, and the mechanisms by which this role occurs. We identify some of the gaps in our knowledge and describe experiments at the Institute of Grassland and Environmental Research, North Wyke (UK) that are attempting to fill some of these gaps. We consider the goals of biodiversity management and some of the important current issues. In the light of these goals, we consider some of the potential management tools that may assist grazing managers to enhance biodiversity.

If we are to exploit current knowledge and to take sensible directions in applied research, it is necessary to consider the goals of our conservation management. To some extent, this is an issue of scale. The goal might be to manage for a cultural landscape, that is not just the physical features of the landscape but also the human aspects.

For example, the species and breed of animal employed might be chosen to reflect traditional local practices. The possibility that this might compromise biodiversity outcomes per se need to be considered. Another goal might be to manage at the habitat level over several different plant communities or at the community level. Alternatively, interest may centre on rare or emblematic species or on the fauna rather than the flora. These scenarios may require very different grazing management practices.

Having established the goals, there is also a need to consider some of the current issues in the management of grasslands for biodiversity. One of these is the need to move away from crude, though easily implemented, management methods such as stocking rates prescriptions on which many current agri-environment schemes are based, to sward based management guidelines such as sward height or sward height distribution [5]. Another pressing issue is to obtain reliable evidence about animal breed and background effects as many current management prescriptions rely heavily on anecdotal evidence. There is also a need to integrate biodiversity goals into intensive systems. Currently, many of our agri-environment schemes are aimed at farmers in marginal areas rather than at, for example the intensive dairy farmer.

2. THE ROLE OF THE GRAZING ANIMAL

Most temperate grasslands require periodic defoliation to control succession, if they are not to succeed to scrub and ultimately woodland. Except on very steep or uneven ground, it is usually possible to achieve this defoliation by mechanical harvesting of the herbage. Indeed some communities such as hay meadows have evolved in response to such management. However, the grazing animal has a unique role to play. This is to maintain and enhance structural heterogeneity of the sward canopy, which in turn has a vital influence on floral and faunal diversity.

3. MECHANISMS FOR CREATING HETEROGENEITY IN GRAZED SWARDS

Probably the most important mechanism by which grazing animals create sward heterogeneity is selective defoliation as a result of dietary choices both between species and between plant parts within species. This alters the competitive advantage between plant species both by direct removal of phytomass and by altering the light environment and competition for soil nutrients [3]. A second mechanism is treading which opens up regeneration niches for gap-colonising species. A third mechanism is nutrient cycling. This has the effect of concentrating nutrients into 'hot spots' at dung and urine patches and again may alter the competitive advantage between species, both directly and by feedback effects on dietary choice and thus on heterogeneity, as cattle in particular will not graze near dung patches. Grazing animals also have a role in propagule dispersal. This may be either endozoochorous (i.e. by seeds passing through the animal's digestive system) or exozoochorous (i.e. by seeds attaching to the animal's coat) dispersal but we particularly stress the role of the endozoochorous route as the mower can also effectively distribute many exozoochorous species. For a more comprehensive review of plant responses to grazing see [2].

The direct effects of grazing on sward canopy structure and the plant community lead to secondary effects on faunal diversity both by changing the abundance of food plants and by providing breeding sites. The direct effects on invertebrate diversity feed through to vertebrate diversity (e.g. [20]). Another secondary effect of the changes in structure and community brought about by grazing is the feedback on the grazing behaviour of the animals by changing the choices available to them.

4. DIETARY CHOICES

Since much of the system is driven by the animal's dietary choices (both between species and between potential feeding stations), it is important to understand the mechanisms driving these choices. It should be stressed that most of our knowledge is derived from simple model systems, such as perennial ryegrass-white clover and that there has been relatively little detailed work in more complex communities, at least in temperate lowland environments.

Generally, behavioural ecologists have assumed that the animal is striving to optimise its evolutionary fitness. In the context of foraging, rate of energy intake has usually been taken as a surrogate measure for evolutionary fitness [18]. However, in many situations animals appear to behave sub-optimally. For example, grazed grass has a carbon/nitrogen ratio too low to be optimal for the animal's requirements but both cattle and sheep offered a free choice with minimal physical constraints consistently chose a diet containing around 70% clover, with an even lower C/N ratio [17]. Furthermore, the mixed diet is not due to intake rate maximisation since in this case animals would choose 100% clover as this species can be eaten faster [17]. This suggests that rate of energy intake is not the currency that the animal is optimising, and that the true currency remains to be identified. To optimise fitness the animal has to trade-off many currencies, for example nutrient intake with predation risk and these trade-offs are not fully understood [17]. These limitations to our knowledge make it difficult to extrapolate from our simple model systems to the more complex swards of interest to biodiversity managers.

In discussing dietary choices, many people, particularly those working in conservation management use the term 'palatability' as a plant descriptor. Unfortunately, the term has been so misused as to have become almost meaningless. Palatability refers to the acceptability to an animal of a food based purely upon organoleptic properties independent of post-ingestive consequences. Animals can learn to associate post-ingestive consequences (for example toxicity) with the taste of a food and subsequently use taste as a cue to avoid this food but there are relatively few examples of choices being made solely on organoleptic grounds. Palatability is primarily an animal not a food characteristic as there are many situations in which an animal's food choice is altered even though the foods themselves remain unchanged. We therefore recommend that the term is not used as a food descriptor and suggest that it is of little use in understanding the basis of dietary choices (for a fuller discussion see [14]).

It is more useful when describing food choices to regard the animal as having a potential intake but being constrained by various factors, including those inherent to the food. When grazing there are important physical constraints on intake and therefore on the choices between plants with different levels of these constraints. These constraints include sward structure (sward height, leafiness, tiller density and horizontal patchiness) and plant physical defence mechanisms (for review see [15]). This latter may be a driving force in patch formation in some situations, for example, the animals may avoid an area around *Cirsium* sp.

Dietary choice changes over time at all scales. This is due to the availability of herbage, phenology of the plant and the physiological state of the animal. An example of a relatively short-term temporal effect is the change in preference between grass and clover that has been observed over the day. Both dairy cows and sheep include more clover in the diet in the morning and more grass in the evening [16]. It has been speculated that this might be either due to higher sugar levels in the grass at this time [11] and hence higher digestibility or, alternatively, it may be because the animal fills its rumen with relatively slowly digesting material (compared to clover) in order to maintain rumen microflora populations during the overnight fast. At present, it is not possible to offer a definitive answer. If a similar circadian effect was to be seen in choices between elements of plant communities of interest for biodiversity, it might be possible to exploit the effect to manipulate overall choice and hence effect on sward structure and diversity.

There are also spatial effects at many scales. Most animals in lowland systems in Europe have no opportunity to make choices at the landscape scale and hence much of our research in these systems relates to choice at the bite or feeding station (i.e. without moving the legs) scale. In hill and upland systems (and range systems in other countries), we know that animals establish home ranges within which they move on daily and longer time scales. Choice of location may be driven by other factors than food, such as water, shelter and social cohesion (itself an anti-predation strategy) (e.g. [6]).

5. ANIMAL TYPE

Animal type has a major effect on dietary choice. The most fundamental effect is that of body size. Because larger animals have relatively large gut capacity in relation to their metabolic requirements, they can retain digesta in the tract for longer and thus digest it more thoroughly. This means that they can deal with a lower digestibility diet and hence can forage less selectively than smaller animals which must of necessity select higher quality items [10]. The animal's physiological state will also affect its selection. For example, hungry animals are less selective [12].

Species effects are of great importance. Some of these are driven by body size, for example, sheep are more selective than cattle. Digestive physiology is also important, for example, ruminants such as cattle have more efficient digestion than hind-gut fermenters such as horses [10]. The latter therefore rely on high throughput and this can necessitate long grazing times of up to 19 hours per day (e.g. [4]). Dental anatomy is also important; horses, with both top and bottom incisors can graze much closer to the ground than cattle and appear to concentrate their grazing in short areas that represent only a small proportion of the available area and thus produce a quite different sward structure [7]. The extent to which grazing by horses results in a different plant community to grazing by cattle is still the subject of some debate. Many horse grazed pastures are overstocked, leading to poor structure and loss of diversity [1]. This has probably resulted in an unjust, negative perception of grazing by horses as a tool for conservation management.

There is much anecdotal evidence (e.g. [19]) for breed differences in diet selection and hence in impact on sward structure and composition but little experimental evidence. In these anecdotal reports, true genetic differences between breeds are often confounded with the environmental effects, particularly prior experience of biodiverse pastures during early life that may affect subsequent selection.

Secondary evidence on breed effects is also patchy. There is some good information about breed and background effects on animal movements at a landscape scale. For example in an experiment in which Scottish Blackface or Suffolk ewes raised either lambs of their own breed or of the other breed [8], the distances between Blackface ewes was greater than between Suffolks but Blackfaces kept their lambs much closer to them, whatever the breed of the lamb. The ewes had a choice of using upland or lowland pasture; the Blackface ewes made much more use of upland and this persisted in the lambs that they had reared whatever the lamb breed, although some effect of lamb breed was also evident (Tab. I).

While we have reasonable information on breed effects on movement at a landscape scale in heterogeneous environments, we know very little about differences at the scale of the grazing bout or feeding patch. There is information from single breeds grazing homogeneous pastures (e.g. [9, 13]); these provide information on parameters such those shown in Table II that allow the development of patchiness in the grazed sward to be reconstructed [2]. However, we have no idea if and how breeds differ in these parameters, how any such effects would be modified in heterogeneous pastures or how they would interact with the background of the animals, either immediately prior to moving to the target area or during early life. It is also possible that small-scale selection and the heterogeneity this creates will differ depending on the scale of enclosure in which the animal is allowed to make its choices. Some of the main gaps in our knowledge are summarised in Table III. Because of these gaps, we are currently ill-placed to predict effects of different grazing managements and breed on biodiversity.

6. CURRENT EXPERIMENTS

In this section, we describe two recently initiated experiments which illustrate research approaches to some current issues in biodiversity management. In an EU project (FORBIOBEN), we are comparing North Devon (a traditional breed) with Charolais × Holstein-Frieisan (a commercial breed) yearling steers. The aim of this project is to test if there are any breed differences in grazing behaviour and impact on biodiversity. With the commercial breed, we will also look at grazing intensity. The animals are grazing agriculturally semi-improved grassland and rush pasture containing 5–10 species per m^2. We have chosen the North Devon as it was originally developed on this type of grassland, particularly rush pastures. We are monitoring botanical structure and flora and faunal diversity, herbage and animal production and economic outputs. Similar trials are taking place at 4 other sites across Europe (Tab. III).

In a second project (BEFORBIO), funded by the UK Department for the Environment, Food and Rural Affairs, we are attempting to separate true breed (genetic) effects from the effects of early experience. North Devon or Hereford-Friesian suckler cows have been mated to North Devon and Charolais bulls, respectively. At birth we

Table I. Inter-animal distance and percentage of time spent on upland pasture by Scottish Blackface and Suffolk ewes rearing lambs either of their own, or of the other breed (according to Dwyer and Lawrence [8]).

Ewe Lamb	Blackface Blackface	Suffolk Blackface	Blackface Suffolk	Suffolk Suffolk
Ewe-ewe distance (m)	12.77	5.30	12.01	3.84
Ewe-lamb distance (m)	6.03	11.64	5.45	10.88
% upland use (ewes)	78	10	82	2
% upland use (lambs)	82	28	55	4

Table II. Examples of small scale (within head down grazing bout) movement parameters for heifers and ewes. According to Harvey et al. [9].

	Heifers	Ewes
Bout duration (s)	180	51
Distance moved during bout (m)	7.3	1.8
Bites per m	32.3	37.4
Bites per bout	244	67
Bites per min	80	79
Bite area (cm^3)	36.4	16.7

Table III. Gaps in current knowledge on the effects of grazing on biodiversity.

Dietary choices of animals in temperate multi-species swards
Small scale animal movements in heterogeneous swards
Relative importance of genetics and environment
Effects of spatial scale at which grazing management is applied

will cross-foster half the calves onto cows of the other breed. Devon cows with their own or fostered calves will graze a fen meadow/rush pasture while Hereford-Friesian cows + calves will graze a fertilised ryegrass sward. In their second year, all the calves will graze on fen meadow/rush pasture and we will compare behaviour and impact on the sward of the different breeds and backgrounds.

7. MANAGEMENT OPTIONS

In this section, we consider some of options for biodiversity management that we believe current research findings in grazing behaviour make possible. We believe there is a need for 'designer animals' that are chosen to deliver desired grazing behaviour and hence biodiversity goals. This might be achieved by exploiting the animal's genetics. We do not believe that genetically modified animals per se will be acceptable to European consumers in the foreseeable future, particularly in a conservation context. However, the new insights provided by genomic technologies open up opportunities for greater understanding of the genetic basis of behaviour and the use of marker

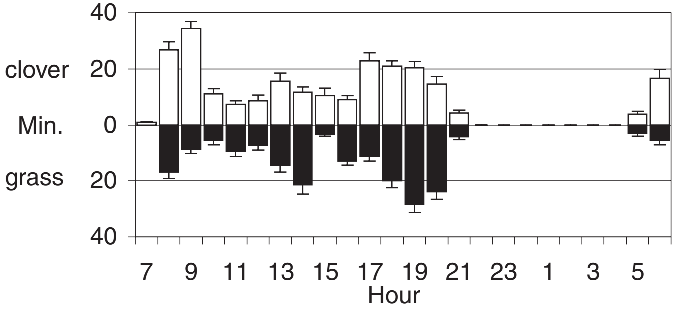

Figure 1. Minutes grazing clover or grass by dairy cows in each hour of the day (according to Rutter et al. [18]).

assisted selection to obtain animals with desirable traits. In the short term, we believe there is opportunity to better exploit the background of animals and to train them to produce the biodiversity outcomes that we desire. There is also much scope for exploiting temporal behaviour patterns to manipulate dietary choices so as to ensure that, whilst animals are productive and provide the farmer with an acceptable economic return, they also make the desired choices when grazing biodiverse pastures. An extreme example of this might be the use of folding systems (such as practised in the past in many chalk downland systems) in which animals are removed to fallow arable land for part of the day as a means of exporting nutrients.

8. CONCLUSIONS

In conclusion, grazing animals have a vital role to play in the management of biodiverse pastures. However, major gaps in our knowledge of grazing behaviour in such pastures and its impact on biodiversity remain. We believe that there is a need for stronger integration between research on plant ecophysiology and plant community ecology and the behavioural ecology of foraging herbivores in order to address these knowledge gaps.

ACKNOWLEDGEMENTS

We thank the organisers of the Pasture Ecology Group Meeting for inviting us to prepare this paper and INRA for funding attendance at the Meeting. We acknowledge funding from the EU Commission Framework 5 programme (FORBIOBEN – QLK5-2001-00130) and from the UK Department for the Environment, Food and Rural Affairs. We also acknowledge the contribution of our partners to the setting up of the FORBIOBEN project – M. Petit, B. Dumont, J. Isselstein, M. Hofmann, K. Osoro, M.F. Wallis de Vries, G. Parente, S. Venerus, M. Scimone, P. Gaskell and J. Mills. Animal Research at IGER is carried out in accordance with the welfare standards approved by IGER's Ethical Review Procedure.

REFERENCES

[1] Bullock D.J., Armstrong H.M., Grazing for environmental benefits, in: Rook A.J., Penning P.D. (Eds.), Grazing management, The principles and practice of grazing, for profit and environmental gain, within temperate grassland systems, British Grassland Society, Reading, UK, 2000, pp. 191–200.

[2] Baumont R., Dumont B., Carrère P., Pérochon L., Mazel C., Design of a multi-agent model of a herd of ruminants grazing a perennial grassland: the animal sub-model, in: Durand J.J., Emile J. C., Huyghe C., Lemaire G. (Eds.), Multi-function grasslands: quality forages, animal products and landscapes, Association Française pour la Production Fourragère, Versailles, 2002, pp. 236–237.

[3] Bullock J.M., Marriott C.A., Plant responses to grazing and opportunities for manipulation, in: Rook A.J., Penning P.D. (Eds.), Grazing management, The principles and practice of grazing, for profit and environmental gain, within temperate grassland systems, British Grassland Society, Reading, UK, 2000, pp. 17–26.

[4] Crowell-Davis S.L., Houpt K.A., Carnevale J., Feeding and Drinking behavior of mares and foals with free access to pasture and water, J. Anim. Sci. 60 (1985) 883–889.

[5] Diack I.A., Burke M., Peel S., Grassland management for nature conservation towards a consistent approach to sward measurement and description, in: Rook A.J., Penning P.D. (Eds.), Grazing management, The principles and practice of grazing, for profit and environmental gain, within temperate grassland systems, British Grassland Society, Reading, UK, 2000, pp. 155–156.

[6] Dumont B, Boissy A., Grazing behaviour of sheep in a situation of conflict between feeding and social motivations, Behav. Processes 49 (2000) 131–138.

[7] Dwyer C.M., Lawrence A.B., Effects of maternal genotype and behaviour on the behavioural development of their offspring in sheep, Behaviour 137 (2000) 1629–1654.

[8] Fleurance G., Duncan P., Mallevaud B., Daily intake and the selection of feeding sites by horses in heterogeneous wet grasslands, Anim. Res. 50 (2001) 149–156.

[9] Harvey A., Parsons A.J., Orr R.J., Rutter S.M., Rook A.J., Movement patterns of sheep and cattle within and between continuous short-term grazing bouts, Proceedings of the 32nd International

Congress of the ISAE, Clermont Ferrand, 21-25 July 1998, p. 215.

[10] Illius A.W., Gordon I.J., Diet selection in mammalian herbivores: constraints and tactics, in: Hughes R.N. (Ed.), Diet selection: an interdisciplinary approach to foraging behaviour, Blackwell Scientific, Oxford, 1993, pp. 157–181.

[11] Orr R.J., Rutter S.M., Penning P.D., Rook A.J., Matching grass supply to grazing patterns for dairy cows, Grass For. Sci. 56 (2001) 352–361.

[12] Newman J.A., Penning P.D., Parsons A.J., Harvey A., Orr R.J., Fasting affects intake behaviour and diet preference of grazing sheep, Anim. Behav. 47 (1994) 185–193.

[13] Roguet C., Prache S., Influence of forage availability on feeding station behaviour of ewes, Ann. Zootech. 44 (Suppl.) (1995) 106.

[14] Rook A.J., Penning P.D., Rook A.J., Limitations to palatability as a concept in food intake and diet selection studies, in: Forbes J.M., Lawrence T.L.J., Rodway R.G., Varley M.A. (Eds.), Animal choices, British Society of Animal Science Occasional Symposium 20, British Society of Animal Science, Edinburgh, 1997.

[15] Rook A.J., Principles of foraging and grazing behaviour, in: Hopkins A. (Ed.), Grass, its production and utilization, 3rd ed., Blackwell Science, Oxford, 2000, pp. 229–241.

[16] Rutter S.M., Orr R.J., Rook A.J., Dietary preference for grass and white clover in sheep and cattle: an overview, in: Rook A.J., Penning P.D. (Eds.), Grazing management, The principles and practice of grazing, for profit and environmental gain, within temperate grassland systems, British Grassland Society, Reading, UK, 2000, pp. 73–78.

[17] Rutter S.M., Orr R.J., Penning P.D., Yarrow N.H., Champion R.A., Atkinson L.D., Dietary preference of dairy cows grazing grass and clover. Proceedings of the Winter Meeting of the British Society of Animal Science, Scarborough, UK, 23-25 March 1998, p. 51.

[18] Stephens D.W., Krebs J.R., Foraging Theory, Princeton University Press, Princeton, 1986.

[19] Tolhurst S., Oates M., The breed profiles handbook, English Nature, Peterborough, UK, 2001.

[20] Vickery J.A., Tallowin J.R., Feber R.E., Asteraki E.J., Atkinson P.W., Fuller R.J., Brown, V.K., The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources, J. Appl. Ecol. 38 (2001) 647–664.