Foraging in patchy grasslands: diet selection by sheep and cattle is affected by the abundance and spatial distribution of preferred species

Bertrand Dumont, Pascal Carrère, P. d'Hour

Anim. Res. 51 (2002) 367–381

DOI: 10.1051/animres:2002033

Original article

Foraging in patchy grasslands: diet selection by sheep and cattle is affected by the abundance and spatial distribution of preferred species

Bertrand DUMONT[a]*, Pascal CARRÈRE[b], Pascal D'HOUR[c]

[a] INRA, Unité de Recherches sur les Herbivores, Theix, 63122 St-Genès-Champanelle, France
[b] INRA, Unité d'Agronomie, Domaine de Crouël, 234 avenue du Brezet, 63039 Clermont-Ferrand 2, France
[c] INRA, Domaine des Monts-Dores, Les Razats, 63820 Laqueuille, France

(Received 22 March 2002; accepted 10 October 2002)

Abstract — Understanding the distribution of grazing activity and its management is valuable to ensure the sustainability and productivity of heterogeneous grasslands. Controlled behavioural studies can provide insight into the cognitive abilities of herbivores and suggest new approaches to improve their grazing distribution. We compared the behaviour and diet selection of sheep and cattle in 1-ha fescue (*Festuca arundinacea* S.) plots, in which the number and size of preferred ryegrass (*Lolium perenne* L.) patches were varied. Five different patterns were used to investigate the effects of ryegrass abundance and spatial distribution on the searching success of the herbivores. Both heifers and ewes grazed ryegrass more when its abundance increased from 1.5 to 6% , and also when ryegrass was aggregated into a few 8×9-m patches, rather than being dispersed into a larger number of 3×3-m ones. Neither the interaction between ryegrass abundance and patch size, nor that between herbivore species and patch size was significant. At 6% abundance, aggregating ryegrass into a single 24×24-m patch tended to further increase its use by heifers, but not by ewes. Fescue less than 1 meter from the nearest ryegrass patch was usually selected more than the fescue located further away. Fescue between 1 and 5 m from the nearest patch was never selected more than the fescue located further away. Our results, together with those for the diet selected by sheep, cattle and deer, when offered patches of a preferred food in aggregated or dispersed patterns, indicate that over a wide range of abundance, it is advantageous for herbivores to forage on patchy resources when the preferred vegetation is aggregated. This corroborates the prediction that foraging costs associated with patch distribution are involved in determining diet selection in patchy grasslands, but our results suggest that it is also influenced by some social characteristics of the animals, such as their social attraction and social tolerance.

aggregation / grazing costs / herbivores / management / social behaviour / spatial memory

* Correspondence and reprints
Tel.: +33 (0)4 73 62 46 07; e-mail: dumont@clermont.inra.fr

Résumé — Dans une mosaïque de végétation, les choix des ovins et des bovins varient selon l'abondance mais aussi la distribution spatiale des placettes préférées. La compréhension des mécanismes qui gouvernent l'utilisation de pâturages hétérogènes permet de proposer des pistes pour conduire les parcelles et les troupeaux au mieux des attendus de l'élevage et de la préservation de la biodiversité. Les études comportementales en situation contrôlée peuvent aussi nous éclairer sur les capacités cognitives des herbivores. Ici, nous avons comparé le comportement et les choix alimentaires de génisses et d'agnelles dans des parcelles de fétuque (*Festuca arundinacea* S.) d'un hectare, dans lesquelles ont été implantées des placettes préférées de ray-grass (*Lolium perenne* L.) de différentes tailles et en différents nombres. Cinq combinaisons d'abondance et d'agrégation du ray-grass ont été proposées aux animaux. Ceux-ci ont plus sélectionné le ray-grass lorsque son abondance augmentait de 1,5 à 6 % . Ils l'ont également plus sélectionné lorsqu'il était agrégé en quelques placettes de 8×9 mètres plutôt que dispersé en de nombreuses placettes de 3×3 mètres, et ceci indépendamment de l'abondance du ray-grass et de l'espèce animale. Au niveau d'abondance supérieur, l'agrégation du ray-grass en une unique placette de 24×24 mètres a semblé augmenter sa consommation par les génisses, mais pas par les agnelles. Seule la fétuque située dans le premier mètre autour des placettes de ray-grass a été plus sélectionnée que la fétuque à distance des placettes. La plus forte exploitation de placettes préférées distribuées en agrégats plutôt que disséminées sur toute la surface de la parcelle semble indépendante de l'abondance relative de ces placettes et de l'espèce d'herbivore qui les exploite. Ceci corrobore la prédiction que les coûts de sélection liés à la distribution spatiale des couverts déterminent pour partie le régime des herbivores dans une mosaïque de végétation. Nos résultats suggèrent que l'exploitation de ces mosaïques est également sous l'influence de facteurs sociaux, tels que l'attraction et la tolérance sociale.

agrégation / comportement social / conduite du pâturage / coût de recherche alimentaire / herbivores / mémoire spatiale

1. INTRODUCTION

In both agricultural and natural grasslands, herbivores forage in spatially complex environments, where resources vary in their attractiveness to herbivores in space and time [11]. Patches occur in most natural grasslands, but also form in more homogeneous swards when forage availability is sufficient for herbivores to graze selectively, and considerable variation may arise in how these patches are spatially distributed [26]. Researchers have recently invested a considerable effort in understanding the spatial aspects of plant-herbivore interactions and their underlying mechanisms [20, 22]. Grazing herbivores are known to discriminate and select amongst patches of different vegetation types, however, there is still little knowledge on how the distribution of preferred patches can affect their behaviour.

Initial research on patchy environments used pelleted foods, grouped together to create different levels of aggregation. Both sheep [17] and cattle [24] consume more of the preferred pellets at larger scales of aggregation. At pasture, an early attempt by Armstrong et al. [1] showed no effect of the spatial distribution of the preferred inter-mixed perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) patches within ryegrass plots on the diet selected by the lambs. Greater effects might be expected in situations where the preferred patches are more abundant and more apparent, thus allowing the animals to walk directly from one preferred patch to another. In plots of heather (*Calluna vulgaris* L. Hull) containing 20% by area of *Agrostis/Festuca* sward, sheep graze heather more when the grass is fragmented into 12 patches [10]. In mosaics of short and tall *Setaria lutescens* grass patches present in equal proportions but

differing in the size of each patch type (fine: 2 × 2 m vs. coarse: 5 × 5 m), cattle select more the preferred short, high quality patches, when grain size is coarse [37]. Recently, Dumont et al. [14] showed that the spatial distribution of a preferred and rare plant species in a cryptic environment can also affect the searching success of sheep: 136 preferred 30 × 30 cm perennial ryegrass patches, covering 0.2% of a cocksfoot (*Dactylis glomerata* L.) plot, were less heavily exploited when evenly dispersed through the sward than when grouped into eight feeding sites. The use of spatial memory has been demonstrated, and it is assumed to act jointly with area concentrated searching and social facilitation, to explain the greater use of the aggregated ryegrass patches.

In spatially complex environments, the responses of different herbivore species to spatial features of the food resource also need to be more fully studied. Direct comparisons of how the behaviour of different herbivores is affected by resource distribution have only been made in grass/heather communities; these showed differences in the way that sheep and deer respond to fragmentation of the resource [10, 19]. Computer simulations suggest a strong interaction between patch abundance and distribution on the searching success of different types of foragers [7, 29, 36]. WallisDeVries [36] showed that herbivores are only affected by the spatial distribution of vegetation patches within a background without forage at low patch densities, i.e. when food patches cover only 1% of this environment. Data of Danell et al. [12] also suggest an interaction between the spatial distribution of sapling strands and the abundance of Scots pine (*Pinus sylvestris*) within these strands, on pine consumption by moose. Rodway-Dyer et al. [30] explored the underlying mechanisms for this phenomenon, by testing the hypothesis that herbivores make different use of their spatial memory depending on resource density. From a theoretical point of view, recent work with the Optimal Foraging Theory has stressed the need to address constraints on the acquisition and processing of information by the animal [23, 29], which also makes it useful to provide new insights into how the spatial distribution of a preferred resource can affect grazing behaviour in herbivores. Here, we compared behaviour and diet selection by sheep and cattle in fescue (*Festuca arundinacea* S.) plots, in which the number and size of the preferred perennial ryegrass patches were varied. Ryegrass covered either 6% or 1.5% of the plot area, and was either aggregated into a single large patch, aggregated into a few medium-sized patches or dispersed into many small patches. Since the plots were kept at a uniform height, only a little cue was available to the animals for locating the patches. This enabled us to discuss the effects of the abundance and spatial distribution of a preferred species on the searching success of grazing herbivores.

2. MATERIALS AND METHODS

2.1. Animals, study site and swards

The experiment was conducted during two consecutive summers (1999 and 2000) in an upland area of central France at the INRA farm of Laqueuille (45°65'N, 2°77'E; altitude 1100 m; annual rainfall 1200 mm). It ran from 8 July to 17 August in 1999 and from 6 July to 16 August in 2000. Twenty 12- to 14-month-old, non-pregnant Limousine ewe-lambs and twenty 18-month-old, non-pregnant Charolais heifers were used each year. The ewes weighed 47 (s.d. 4.1) kg in 1999 and 34 (s.d. 2.2) kg in 2000; the ewes in 2000 being two months younger but with similar grazing experience. The heifers weighed 415 (s.d. 21) kg in 1999 and 467 (s.d. 30) kg in 2000.

A fescue-dominated (cv. Florine) pasture was divided into eight plots of approximately 1 ha, in which perennial ryegrass

(cv. Herbie) was sown in patches where fescue had been removed. The preference measurements between the same two cultivars, also made with dry ewes, indicated that the ewes spent 0.71 of their time grazing ryegrass [28]. Here, the number and size of the ryegrass patches were varied in the different plots, resulting in five different abundance and distribution patterns (Fig. 1). Ryegrass covered either 6% or 1.5% of the plot area, and was either aggregated into a single 24 × 24 m patch (H.Ag. for 6% abundance only), aggregated into a few 8 × 9 m patches (Ag.), or dispersed in many 3 × 3 m patches (Disp.). The number of patches varied according to the treatments: 1, 8 or 64 for 6% abundance, 2 or 16 for 1.5%.

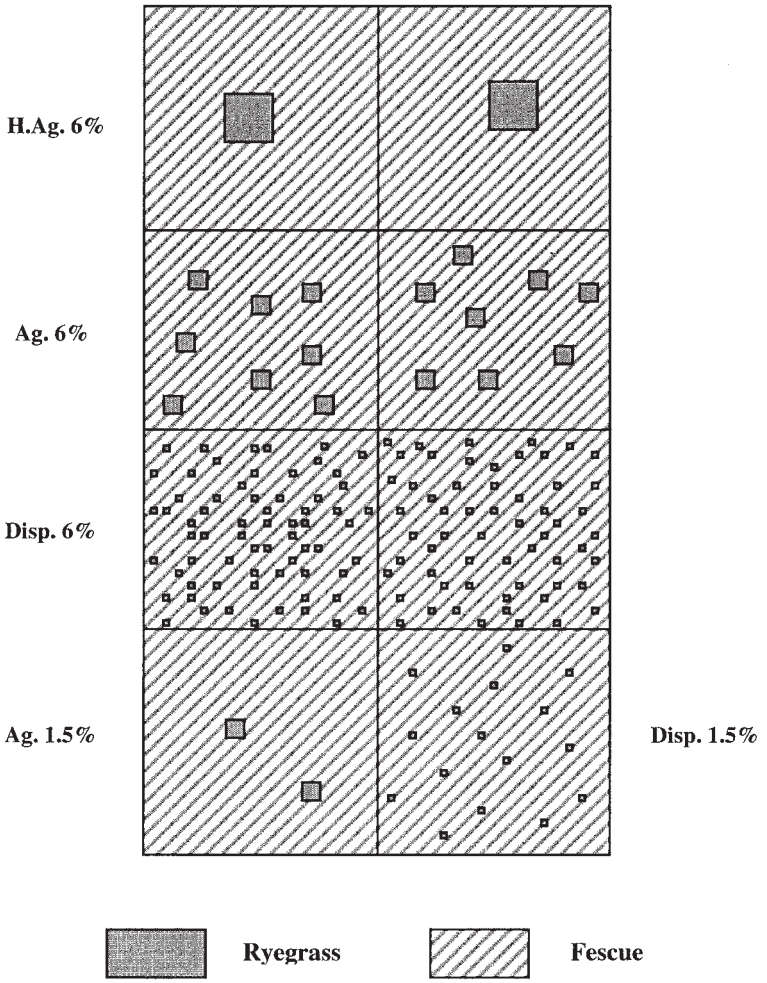

Figure 1. The layout of the experimental site, showing the eight plots and five treatments. Ryegrass covered either 6% or 1.5% of the plot area, and was either aggregated into a single 24 × 24 m patch (H.Ag. for 6% abundance only), aggregated into a few 8 × 9 m patches (Ag.), or dispersed in many 3 × 3 m patches (Disp.).

The fescue was sown in the spring of 1997, while ryegrass patches were established in the spring of 1998. Slurry was sprayed on the whole pasture at a rate of 40 $t \cdot ha^{-1}$ in March 1999, with another 30 $t \cdot ha^{-1}$ being put on in January 2000. Early-spring nitrogen fertilization was also slightly reduced in the second year. To estimate the standing dry matter of the two sward types (Tab. I), twenty-seven 1 m × 0.1 m strips were cut 0.5 cm from the ground level with electrically powered shears in September 1999 and August 2000, and the grass was oven-dried at 80 °C for 48 h. At the same period, 1 000 measurements were randomly made in the fescue and another 260 in the ryegrass to estimate the sward botanical composition, by recording the first contact of a stick with the sward surface. Due to the invasion of *Poa pratensis* in the experimental plots (Tab. I), we decided to fertilise ryegrass patches with 30 kg $N \cdot ha^{-1}$ at the beginning, middle and end of each experimental period, in order to maintain their attractiveness. Consequently, the ryegrass had an NDF content similar to that of fescue, but a higher crude protein content and a higher organic matter digestibility (Tab. I).

2.2. Measurement schedule

Both the heifers and ewes were tested in stable groups of five animals, and had never grazed the plots before the measurements began. Since dietary preferences of herbivores can be affected by their recent diet, the animals were maintained on an adjacent cocksfoot plot of intermediate quality when not being tested. There were two measurement days each week. Two or three days before measurements were made, the plots were mown to a height of 4 cm and allowed to grow back to 6–7 cm. Sward height was defined as the first contact of a point with the undisturbed surface of the sward, fifty random measurements being taken on ryegrass and on fescue before each test. The average heights were similar between treatments (Tab. II): the sward was slightly higher in the ryegrass patches (6.83 (s.d. 0.15) cm) than the fescue (6.12 (s.d. 0.11) cm) due to a greater leaf appearance rate in the ryegrass compared to the fescue, further enhanced by the additional N-fertilization received by the ryegrass.

On measurement days, a group of heifers and a group of ewes were simultaneously tested on two different treatments in the morning, two new groups being tested on two other treatments in the afternoon. Each year, we used a partially balanced design in an incomplete Latin square, to randomise the 10 treatments (5 patch distributions × 2 species) over the 10 measurement days, so that each group was tested once on each treatment by the end of the experimental period. Each treatment was performed twice in the morning and twice in the afternoon. On each measurement day, the animals were allowed to graze until 08.00 h in the morning and were then kept in a barn with no access to food. From 09.00 h, the two groups that were being tested were observed grazing in the experimental plots until 11.30 h. All the animals were then turned out onto the cocksfoot plot until 13.00 h, penned up again for one hour, after which two more groups were observed grazing in the experimental plots until 16.30 h. All the animals were then turned out to pasture, on the cocksfoot plot, until the next measurement day.

2.3. Foraging behaviour and social activity

During the tests, the observers recorded the activity (grazing on ryegrass, grazing on fescue, walking or idling) of each animal visually. The interval between the observations was 3 min. An animal was considered to be grazing when it was either biting or chewing grass, or when it was walking with its muzzle close to the sward. When an animal was grazing on fescue, the observer recorded its distance from a ryegrass patch.

Table I. Main characteristics of the two swards grazed in the experiment.

	Ryegrass		Fescue	
Standing dry matter (tDM·ha^{-1})	2.81 (0.37)[1]		2.49 (0.19)	
Green leaves (% of biomass)	58.0 (2.6)[1]		48.2 (2.6)	
Botanical composition (% of cover)				
	Lolium perenne	79	*Festuca arundinacea*	74
	Poa pratensis	16	*Dactylis glomerata*	9
	Other species	< 5	*Poa pratensis*	7
			Trifolium repens	5
			Other species	< 5
NDF content (g·kg^{-1} DM)[2, 3]	543		547	
Crude protein (g·kg^{-1} DM)[3, 4]				
1999	277		253	
2000	310		212	
OM Digestibility [3, 5]				
1999	0.82		0.74	
2000	0.84		0.67	

[1]Standard error of the mean within parentheses.
[2]Following Goering and Van Soest [18].
[3] Samples taken within the grazed horizon.
[4]Kjeldahl N × 6.25.
[5]Pepsin-cellulase method [2].

Table II. Average sward height (+/– s.e.m.) of ryegrass and fescue in the different treatments for the short-term behaviour observations.

	Heifers			Ewes		
	H.Ag.	Ag.	Disp.	H.Ag.	Ag.	Disp.
Ryegrass height (cm)						
6% abundance	6.94 (0.36)	7.00 (0.44)	7.03 (0.30)	6.75 (0.36)	6.81 (0.33)	6.73 (0.31)
1.5% abundance		6.98 (0.52)	6.61 (0.36)		6.73 (0.32)	6.68 (0.41)
Fescue height (cm)						
6% abundance	6.06 (0.19)	6.20 (0.27)	6.24 (0.26)	5.97 (0.26)	5.99 (0.23)	6.04 (0.23)
1.5% abundance		6.13 (0.33)	6.04 (0.25)		6.23 (0.24)	6.29 (0.28)

H.Ag., Ag., Disp.: see Figure 1 for a description of the treatments; s.e.m.: standard error of the mean.

The fescue surrounding the ryegrass patches was classified into zones, according to the distance from the edge of the nearest patch: 0–1 m, 1–5 m and greater than 5 m. For each test, we calculated a selection index for the ryegrass patches and for each fescue zone. The time animals spent grazing ryegrass and fescue in the different zones was therefore divided by their area in each plot. Three variables were calculated to obtain some additional information on the way that the animals exploited the ryegrass patches. These were the synchronisation in the choice of ryegrass, the number of bouts of ryegrass consumption and the mean length of these bouts [35]. The synchronisation in the choice of ryegrass was calculated each time an animal grazed

ryegrass, as the number of other animals engaged in the same activity (i.e., max. = 4.00). To calculate the number and mean length of ryegrass consumption bouts, we assumed that the activity recorded by scan sampling was the only activity occurring during the 3 min between the scans. Consequently, ryegrass bout length was estimated in minutes as the number of successive scans when an animal was grazing ryegrass, multiplied by 3.

2.4. Long-term sward assessment of foraging

Although there is often a good relationship between the predictions made from short- and medium-term measurements, relying on short-term measurements only, to predict animal-plant interactions, may lead to erroneous conclusions. Accordingly, we extended our short-term behaviour observations by using longer-term sward measurements. We assessed the impact of heifers and ewes over a four-week period of plot use, under continuous grazing on the H.Ag. and Ag. treatments at 6% abundance, by repeated measurements of marked ryegrass and fescue tillers [8]. The measurements were made simultaneously on the two treatments after all the tests had been completed, in 1999 for the heifers and in 2000 for the ewes. For each treatment, the eight measurements were separated by 2- to 4-day intervals, which constituted seven sub-periods. The frequency of the observations was adjusted to the growth of the sward and to the defoliation rate, to minimise the probability of two successive defoliation events occurring on the same tiller between two consecutive observations.

For each grass type, we marked tillers bearing at least two leaves with a visible ligule. At each observation, the status of the leaves (intact, defoliated or dead) was recorded. In the case of defoliated leaves, the lamina tip was marked with a small longitudinal incision, in order to detect any further defoliation. In both plots, marked population units were located along four 50-m long transects. For the H.Ag. plot, the four transects diverged from the centre of the ryegrass patch in the direction of the plot corners. For the Ag. plot, the four transects were located to join the centres of two ryegrass patches. On each transect, there were eight quadrats (0.50×0.25 m), with eight tillers labelled in each quadrat, so that an animal could not defoliate two labelled tillers with a single bite. Quadrats were located at regular intervals, with three quadrats in the ryegrass and five in the fescue for the H.Ag. plots and four quadrats in each grass type for the Ag. plots. The proportion of tillers grazed was calculated from the ratio of defoliated tillers (with at least one leaf defoliated during the sub-period) to the tillers present. Since the stocking density was adjusted to sward growth in order to maintain a constant sward surface height, we could calculate a standardised probability of tiller defoliation for each grass type in each sub-period (i.e., defoliation probability (animal^{-1}·day^{-1}) $\times$ average stocking rate over the four weeks / actual stocking rate over the sub-period [8]).

2.5. Statistical analyses

We used the GLM procedure of the SAS statistical package [33] to analyse data on the proportion of grazing time spent on ryegrass, synchronisation in the choice of ryegrass, number of bouts of ryegrass consumption and mean length of these bouts. We used two models. The first one, on choice data from Ag. and Disp. plots only, comprised the main effects for herbivore species, year, group nested within species and year, ryegrass abundance and patch size, and the interactions between patch size and herbivore species, patch size and year, and patch size and abundance. The second model, on all the behavioural data from 6% abundance plots, comprised the main effects for the herbivore species, year,

group nested within species and year, ryegrass patch size, and the interactions between patch size and herbivore species, and patch size and year. Patch size was taken as a covariate in the latter choice data analysis. The selection for ryegrass and for each fescue zone was determined by the comparison of the average selection indices to unity (no selection, no avoidance) using a one-tailed Student-test. A Wilcoxon test for paired data was used to detect differences in zone utilisation within and between plots. All the short-term behavioural data were analysed for the whole test (i.e., over 2h30'), but also for the first hour of grazing only. For medium-term sward measurements, an ANOVA was performed to compare, within each herbivore species, the effect of ryegrass distribution on the ratio of the defoliation of ryegrass tillers to fescue tillers. Only the means from individual transects (4 replicates) were analysed. Data collected after one week of grazing (i.e. after 2 sub-periods) and after four weeks (i.e. after 7 sub-periods) were considered, the probability of tiller defoliation being averaged over the different sub-periods in the latter case.

3. RESULTS

The statistical analyses gave exactly the same range of *P*-values, whether the measurements were considered for the first hour of grazing or over the whole test. Here we present data for the first hour of grazing only, since ryegrass depletion thereafter could have affected the amplitude of the effects of ryegrass abundance and distribution.

3.1. Choice of ryegrass

During the first hour of grazing (Fig. 2), the animals of both species spent more time grazing ryegrass in Ag. and Disp. plots when its abundance was high (37.0% for 6% vs. 20.8% for 1.5%; $P < 0.001$), and when ryegrass was aggregated into a few medium-sized patches, rather than being dispersed in many small ones (32.3% for Ag. vs. 25.5% for Disp.; $P < 0.05$). There was no significant interaction between ryegrass abundance and patch size, nor between herbivore species and patch size. However, the ewes spent more time grazing ryegrass than the heifers (32.0 vs. 25.8% of grazing time; $P < 0.05$). The animals of both species grazed more ryegrass in the second year trials ($P < 0.001$), without any significant difference between the heifers and between the ewes within a year. The interaction between patch size and year was also not significant.

At 6% abundance, the animals tended to graze ryegrass more when it was aggregated more ($P < 0.08$). Although there was no significant interaction between herbivore species and this aggregation level ($F_{1,29} = 0.69$), aggregating ryegrass into a single large patch tended to increase its utilisation by heifers (37.2% of grazing time for Ag. vs. 44.8% for H.Ag.) but not by ewes (42.6% for Ag. vs. 42.8% for H.Ag.; Fig. 2). Consequently, the heifers and ewes spent

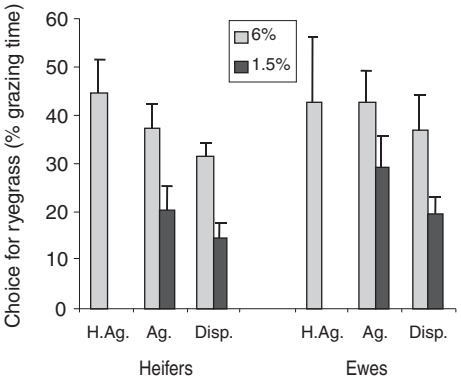

Figure 2. The proportion of grazing time heifers and ewes spent on ryegrass during the first hour of grazing according to ryegrass abundance (1.5 or 6%) and horizontal distribution (H.Ag., Ag., Disp.: see Fig. 1 for the description of the treatments). Vertical bars represent the s.e.m.

approximately the same time grazing ryegrass (37.8% of grazing time for the heifers vs. 40.7% for the ewes; NS), without any difference between the groups. The animals grazed more ryegrass in the second year trials ($P < 0.001$), with a significant interaction between year and ryegrass aggregation level ($P < 0.05$) due to its lower utilisation in the H.Ag. plots in year 1999 by the animals of both species.

3.2. Selection indices

The preference of animals for ryegrass over fescue was confirmed by the selection index measurements (Tab. III). Although the choice of ryegrass was greater at 6% than at 1.5%, the difference was not in the proportion of ryegrass abundance. In the Ag. and Disp. plots, the selection index for ryegrass was indeed, in both heifers and ewes, always at least two times higher when ryegrass was less abundant ($P < 0.05$). The fescue growing less than 1-m from the nearest ryegrass patch was either positively selected by the animals, or at least used in proportion to the area (Tab. III). Fescue less than 1 meter from the nearest ryegrass patch was usually selected more than the fescue located further away, which was either used in proportion to the area or avoided by the animals. Fescue between 1 and 5 m from the nearest patch was never selected more than the fescue located further away.

3.3. Social synchrony

In spite of there being only a tendency for patch distribution to affect the choices at 6% abundance, there were, in both species, clear effects of patch distribution on bout dynamics (Tab. IV). As the ryegrass became more aggregated, the number of bouts of ryegrass consumption decreased ($P < 0.01$) and the mean length of these bouts increased

Table III. Selection indices (mean +/– s.e.m.) for ryegrass patches and fescue zones according to their distance from the nearest ryegrass patch: 0–1 m, 1–5 m and greater than 5 m. These were calculated by dividing the proportion of time grazing in each zone by its relative area. The selection for each of the zones was determined by comparing the averaged data to unity (no selection, no avoidance) using a one-tailed Student *t*-test. A Wilcoxon test for paired data was used to detect the differences in zone utilisation within the plots.

	In patch	0–1 m	1–5 m	> 5 m
Heifers				
H.Ag. 6% abundance	**7.47**a (1.13)	**2.88**b (0.86)	0.81c (0.20)	*0.55*c (0.08)
Ag. 6% abundance	**6.21**a (0.88)	**1.85**b (0.42)	*0.62*c (0.09)	*0.63*c (0.08)
Disp. 6% abundance	**5.22**a (0.51)	0.76b (0.21)	*0.63*b (0.07)	1.07b (0.24)
Ag. 1.5% abundance	**13.4**a (3.26)	**1.70**b (0.34)	*0.59*c (0.15)	*0.82*c (0.05)
Disp. 1.5% abundance	**9.61**a (2.14)	1.56bc (0.65)	*0.45*c (0.07)	0.99b (0.09)
Ewes				
H.Ag. 6% abundance	**7.13**a (2.21)	2.10b (1.28)	0.99b (0.25)	*0.57*b (0.16)
Ag. 6% abundance	**7.10**a (1.13)	1.32b (0.33)	*0.45*c (0.10)	*0.63*bc (0.09)
Disp. 6% abundance	**6.13**a (1.23)	0.85b (0.21)	*0.63*b (0.10)	0.74b (0.28)
Ag. 1.5% abundance	**19.4**a (4.17)	2.59b (1.18)	0.69b (0.26)	*0.71*b (0.08)
Disp. 1.5% abundance	**13.0**a (2.49)	**2.19**b (0.48)	0.86c (0.11)	*0.75*c (0.06)

H.Ag., Ag., Disp.: see Figure 1 for description of treatments.
Data in bold characters are higher than unity ($P < 0.05$), those in italics are lower ($P < 0.05$).
a,b,c: Within each row, the means with different superscripts differ ($P < 0.05$).

($P < 0.05$). Both the heifers and ewes were more synchronised in their choice of ryegrass when the ryegrass was aggregated ($P < 0.001$). There was no significant interaction between the herbivore species and aggregation level. However, the ewes were generally more synchronised than the heifers (3.05 vs. 2.40; $P < 0.001$). The same patterns were observed at 1.5% abundance (Tab. IV).

3.4. Medium-term sward measurements

After one week of continuous grazing, the ratio of defoliation of the ryegrass to fescue tillers tended to be higher in the single aggregated patch for heifers (1.66 for H.Ag. vs. 1.32 for Ag.; $F_{1,6} = 0.40$; NS) but not for ewes (2.29 for H.Ag. vs. 2.51 for Ag.; $F_{1,6} = 0.06$; NS). Over the four weeks of tiller defoliation measurements, the effect of the ryegrass aggregation pattern was similar for the heifers (1.51 for H.Ag. vs. 1.22 for Ag.; $F_{1,6} = 1.28$; NS) and the ewes (2.18 for H.Ag. vs. 1.98 for Ag.; $F_{1,6} = 0.26$; NS).

4. DISCUSSION

4.1. Selection of ryegrass

Both heifers and ewes selected more of the preferred grass when its abundance was 6% compared to 1.5% though the increase in preference was not in the expected ratio 6:1.5 (Fig. 2). At pasture, the vegetation abundance becomes important when the rate of encounter of a preferred species is affected, resulting in different times and energy costs for locating them. For example, it has been widely observed that sheep are constrained in their attempt to obtain a preferred diet when the fractional cover of their preferred species becomes less than about 20% of the plot area [9, 27]. In keeping with this, both heifers and ewes here selected less ryegrass than that observed by Prache et al. [28] in preference tests with sheep (i.e., at 50% ryegrass abundance), and decreasing ryegrass abundance from 6 to 1.5% would be expected to further decrease the proportion of ryegrass in their diet. However, in both heifers and ewes, the selection index for ryegrass was higher

Table IV. Synchronisation in the choice of ryegrass (max. = 4.00), number of bouts of ryegrass consumption and mean length of these bouts in heifers and ewes, according to ryegrass abundance and spatial distribution (mean +/– s.e.m.).

	Heifers			Ewes		
	H.Ag.	Ag.	Disp.	H.Ag.	Ag.	Disp.
Synchronisation						
6% abundance	3.23 (0.12)	2.35 (0.27)	1.63 (0.17)	3.54 (0.12)	3.18 (0.11)	2.49 (0.23)
1.5% abundance		2.16 (0.34)	0.94 (0.11)		3.53 (0.10)	2.52 (0.39)
Number of bouts						
6% abundance	2.6 (0.3)	3.7 (0.4)	3.9 (0.4)	2.2 (0.7)	3.5 (0.5)	3.6 (0.4)
1.5% abundance		2.0 (0.4)	1.9 (0.3)		1.5 (0.3)	2.3 (0.5)
Bout length (min)						
6% abundance	7.7 (0.8)	7.1 (1.0)	6.5 (0.6)	11.6 (2.0)	7.5 (0.8)	6.6 (0.4)
1.5% abundance		10.0 (1.8)	10.1 (1.1)		11.8 (1.1)	9.2 (0.9)

H.Ag., Ag., Disp.: see Figure 1 for the description of treatments.

when ryegrass was less abundant (Tab. III). In this way, our results are entirely consistent with those of Armstrong et al. [1], who showed that selection for clover by sheep was more pronounced when the abundance of grass-clover patches in perennial ryegrass plots decreased.

At both abundance levels, diet selection by heifers and ewes was further affected by the horizontal distribution of ryegrass patches. Both animal species selected more ryegrass when it was aggregated into patches of at least 8 × 9 m, rather than being dispersed into many small patches (Fig. 2). This confirms what has already been observed with sheep in plots where the preferred species was either more [10] or less [14] abundant (20 and 0.2%, respectively). Conversely, the only previous evidence of an effect of patch distribution on the diet selected by cattle came from mosaics of short, high-quality and tall, low-quality patches in equal proportions [37]. Our results extend this finding to more cryptic environments, where the preferred species is also less abundant.

4.2. Foraging costs

Here, we did not observe any interaction between the ryegrass abundance and its horizontal distribution. To further investigate the relationship between the species abundance and patch distribution, we present our results in a figure together with those for the diet selected by sheep [10, 14, 17, 31], cattle [37] and deer [10], when offered patches of a preferred food in aggregated or dispersed patterns at a range of abundance (Fig. 3). In spite of the different amplitudes for sheep and deer in the effect of grass aggregation within a grass/heather mosaic [10], data from all three herbivore species were considered together, since they followed the same trends, even though the foods offered for choice were different. This allowed us to propose a conceptual representation, extending that of Clark and Harris [9], of the relationships between plant abundance and diet selection, by considering the patchy distributions differently according to whether the patches were aggregated or dispersed.

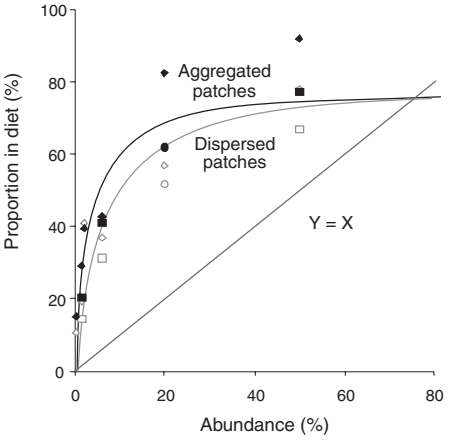

Figure 3. The interaction between the spatial distribution of patches of preferred vegetation (Aggregated = dark symbols vs. Dispersed = open symbols) and its abundance (in % of total area) on the diet selected by sheep (diamonds), cattle (squares) or deer (circles). Data are from Edwards et al. [17] (50% abundance), Clarke et al. [10] (20% abundance), WallisDeVries et al. [37] (50% abundance), Dumont et al. [14, present study] (0.2, 1.5 and 6% abundance) and Sibbald and Hooper [31] (1.6% abundance). We only used the most extreme treatments of Edwards et al. [17] and Sibbald and Hooper [31], since the intermediate ones were difficult to classify as aggregated or dispersed. The two aggregated patterns of Clarke et al. [10] and of the present study were averaged. All data came from short-term (15 min–2 h) measurements, apart from those of Clarke et al. [10] which are on a daily scale. All the results are expressed as the proportion of grazing time, apart from those of Edwards et al. [17] (in % of patches eaten) and WallisDeVries et al. [37] (in % of steps in the patch). Assuming that the preferred diet is a mixture with 76% of the preferred species, regression relationships are $Y = (79.18 \times X) / (X + 3.18)$; $n = 10$; $R^2 = 0.84$ for the aggregated patches and $Y = (82.59 \times X) / (X + 6.59)$; $n = 10$; $R^2 = 0.79$ for the dispersed ones.

The figure conveys clearly how the index of selectivity is greater (in both cases) at low abundances of the preferred vegetation. We can gain some insight into why this might be by reference to simple models of the costs and benefits of foraging. The shape of the figure is consistent with that predicted by Thornley et al. [34] as to what would be the optimal trade off between the benefits of eating the preferred food, and the costs of foraging for this, across a range of abundances. Thornley's account did not consider different spatial arrangements, dispersal or aggregation of food items. However the greater success in eating the preferred grass seen when the food was aggregated into fewer larger patches in the present study, is consistent with what Thornley et al. [34] would predict if the costs of foraging were reduced in the aggregated food patches compared to the more dispersed ones.

There are a number of ways in which the balance of the benefits and costs of foraging would have been altered by the spatial distribution of food into patches. The aggregation of food would have altered both the costs of exploiting (handling) the preferred food, and the costs of finding (searching for) it. It can be assumed that when food is aggregated, the animals concentrate foraging within the preferred area, more than when the food is dispersed [e.g., 14]. Area concentrated foraging greatly improves the exploitation of a patchy resource once it has been found [5]. It is more difficult, however, to conclude how the distribution of patches affected the costs of searching for the preferred patches. The size of the area sampled in the 'field of view' of the animal, and the constraint of walking a path, affect the probability that the preferred area is encountered in any one step, and hence the rate of encounter with preferred patches. At a given level of abundance, the rate of encounter with patches should thus be greater in the dispersed compared to the aggregated patterns [7, 21]. While this is true, it is important to note that the rate of encounter with food within a patch, that is once a patch has been encountered, will conversely be substantially greater in the aggregated patterns compared to the dispersed, such that the random expectation for the rate of encounter with food items (as opposed to patches) is the same in both cases. The greater use of ryegrass in the aggregated patterns even during the first hour of grazing (Fig. 2) suggests that, here, the rate of encounter with patches had a seemingly small effect on foraging success.

4.3. Behavioural mechanisms

The greater overall use of ryegrass in the aggregated patterns can be attributed to a modified behaviour (e.g., area concentrated foraging) within the preferred food patches, and to behaviours animals adopt to return to previously discovered patches. Herbivores quickly learn the distribution of patches with a preferred food at pasture, and this can strongly increase their foraging success. The accuracy of spatial memory is higher as the number of sites that have to be memorized decreases [25]. In a memory task, sheep [15] and cattle [4] have also been shown to remember the amount of food found in the sites and to better exploit those where they were more rewarded. Consequently, here spatial memory should have improved the foraging success of heifers and ewes when ryegrass was aggregated into a few large patches. However, it was probably not the only behavioural mechanism involved, and some social characteristics of the animals could also explain spatial variation in the mosaic utilisation.

In both 1-h tests (Fig. 2) and after a week of continuous grazing, cattle tended to increase their use of ryegrass when it was highly aggregated, whereas the sheep did not. With the highly aggregated patches, an animal wanting to graze ryegrass while its peers were on fescue would often have to

separate from the group. Even if the degree of cohesion between sheep varies with breed [e.g., 16], individual sheep will usually not leave the group to reach a preferred patch located far away, unless they are accompanied by several other peers [13]. This is particularly true for familiar animals: even in Scottish Blackface, a breed characterised by low flocking tendencies [16], more social individuals grazed less when faced with a choice between remaining close to other sheep or moving away to graze [32]. This may explain why the ewes in this experiment did not use the single large ryegrass patch more, and is consistent with the observation that, in the H.Ag. treatment, the ewes were highly synchronised when grazing ryegrass and returned less frequently to the single patch than to patches in the Ag. and Disp. treatments (Tab. IV). With the highly aggregated pattern, heifers were slightly less synchronised than ewes when grazing ryegrass (Tab. IV), with the amplitude of this difference tending to increase during the test (2.99 vs. 3.51 over 2 h 30 min). Consequently, the tendency of heifers to graze ryegrass more when aggregated into a single large patch, may partly be the consequence of cattle having a greater ability to increase inter-individual distances in order to express a preference.

In the dispersed pattern, competition for the small ryegrass patches could have influenced diet selection by the heifers even more, if it was only the dominant individuals that had access to the preferred resource, as is usually observed with penned cattle [6]. Consistently, the heifers were less synchronised than the ewes in their choice of ryegrass with the dispersed pattern, at both abundance levels (Tab. IV). In the study of WallisDeVries et al. [37], grain size in the fine-grained environment was equivalent to the cattle's body length, whereas in the coarse-grained plots several steers may have grazed on the same short, high quality patch. In keeping with our hypothesis, grouping tendency may have forced some animals to graze on the tall, low quality patches in the fine-grained plots, which would partly explain the lesser selection of better quality patches. Similarly, Hester et al. [19] reported that the cost for red deer of grouping within a highly fragmented grass/heather mosaic was that some animals were forced onto the less preferred vegetation, since many patches were too small to accommodate all the animals.

In conclusion, foraging by sheep and cattle in patchy grasslands is thus affected by the number and horizontal distribution of the preferred patches. From a practical point of view, it has frequently been pointed out that there are negative impacts of herbivores clustering around preferred patches, e.g. in grass/heather mosaics [10, 19]. On the contrary, in extensively used grasslands, uneven grazing by herbivores can lead to resource degradation in the areas they seldom exploit. It would therefore be of great benefit to introduce preferred patches of vegetation to encourage the animals to explore the whole paddock, as is already done by providing water, supplement, salt, shade or shelter in under-utilized feeding sites (see [3] for review). For the moment, the optimum size of attractive feeding sites, the best way of distributing them and the stocking rates and paddock sizes at which such practices could have an effect on vegetation dynamics, are poorly understood. A few large patches proved more attractive to the animals than many small ones, but in our study it was only in the first meter around these patches that the fescue was selected more than the fescue located further away, which would limit the value of establishing such patches in paddocks. The benefits of local improvement practices should thus now also be tested in larger areas, where the cost to the animals of exploring the whole paddock is high, and over longer periods to match the ecological time scales of vegetation change.

ACKNOWLEDGEMENTS

We are grateful to S. Valette, R. Chauvet, J.L. Chaput and B. Sepchat for plot sowing, care of the animals and help with measurements, to J. Jamot who did the chemical analyses, and to A.J. Parsons, A.M. Sibbald, M. Petit and A. Boissy for useful comments on an early version of the manuscript. This work was supported by the INRA-AIP pâturage fundings.

REFERENCES

[1] Armstrong R.H., Robertson E., Lamb C.S., Gordon I.J., Elston D.A., Diet selection by lambs in ryegrass-white clover swards differing in the horizontal distribution of clover, in: Proceedings of the XVIIth International Grassland Congress, Palmerston North, New-Zealand, 1993, pp. 715–716.

[2] Aufrère J., Michalet-Doreau B., In vivo digestibility and prediction of digestibility of some hay products, in: Feeding Value of By-Products and Their Use by Beef Cattle, EEC Seminar EUR 8918 EN, 1983, pp. 25–35.

[3] Bailey D.W., Dumont B., WallisDeVries M.F., Utilization of heterogeneous grasslands by domestic herbivores: Theory to management, Ann. Zootech. 47 (1998) 321–333.

[4] Bailey D.W., Rittenhouse L.R., Hart R.H., Swift D.M., Richards R.W., Association of relative food availabilities and locations by cattle, J. Range Manage. 42 (1989) 480–482.

[5] Benhamou S., Spatial memory and searching efficiency, Anim. Behav. 47 (1994) 1423–1433.

[6] Bouissou M.F., Boissy A., Le Neindre P., Veissier I., The social behaviour of cattle, in: Keeling L.J., Gonyou H.W. (Eds.), Social Behaviour in Farm Animals, CAB International, Wallingford, UK, 2001, pp. 113–145.

[7] Cain M.L., Random search by herbivorous insects: a simulation model, Ecology 66 (1985) 876–888.

[8] Carrère P., Louault F., Soussana J.F., de F. Carvalho P.C., Lafarge M., How does the vertical and horizontal structure of a grass and clover sward influence grazing?, Grass For. Sci. 56 (2001) 118–130.

[9] Clark D.A., Harris P.S., Composition of the diet of sheep grazing swards of differing white clover content and spatial distribution, N.Z. J. Agric. Res. 28 (1985) 233–240.

[10] Clarke J.L., Welch D., Gordon I.J., The influence of vegetation pattern on the grazing of heather moorland by red deer and sheep. I. The location of animals on grass/heather mosaics, J. Appl. Ecol. 32 (1995) 166–176.

[11] Coughenour M.B., Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems, J. Range Manage. 44 (1991) 530–542.

[12] Danell K., Edenius L., Lundberg P., Herbivory and tree stand composition: moose patch use in winter, Ecology 72 (1991) 1350–1357.

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

[14] Dumont B., Maillard J.F., Petit M., The effect of the spatial distribution of plant species within the sward on the searching success of sheep when grazing, Grass For. Sci. 55 (2000) 138–145.

[15] Dumont B., Petit M., Spatial memory of sheep at pasture, Appl. Anim. Behav. Sci. 60 (1998) 43–53.

[16] Dwyer C.M., Lawrence A.B., Ewe-ewe and ewe-lamb behaviour in a hill and a lowland breed of sheep: a study using embryo transfer, Appl. Anim. Behav. Sci. 61 (1999) 319–334.

[17] Edwards G.R., Newman J.A., Parsons A.J., Krebs J.R., Effects of the scale and spatial distribution of the food resource and animal state on diet selection: an example with sheep, J. Anim. Ecol. 63 (1994) 816–826.

[18] Goering H.K., Van Soest P.J., Forage fiber analyses, in: Agricultural Handbook No. 379, US Department of Agriculture, Washington, DC, 1970, pp. 1–20.

[19] Hester A.J., Gordon I.J., Baillie G.J., Tappin E., Foraging behaviour of sheep and red deer within natural heather/grass mosaics, J. Appl. Ecol. 36 (1999) 133–146.

[20] Hobbs N.T., Response of large herbivores to spatial heterogeneity in ecosystems, in: Jung H.-J.G., Fahey G.C. Jr. (Eds.), Nutritional Ecology of Herbivores, Proceedings of the Vth International Symposium on the Nutrition of Herbivores, American Society of Animal Science, Savoy, IL, 1999, pp. 97–129.

[21] Kershaw K.A., Quantitative and Dynamic Plant Ecology, 2nd ed., Elsevier, New York, 1973.

[22] Laca E.A., Modelling spatial aspects of plant-animal interactions, in: Lemaire G., Hodgson J., de Moraes A., Nabinger C., de F. Carvalho P.C. (Eds.), Grassland Ecophysiology and Grazing Ecology, CAB International, 2000, pp. 209–231.

[23] Laca E.A., Demment M.W., Foraging strategies of grazing animals, in: Hodgson J., Illius A.W. (Eds.), The Ecology and Management of Grazing Systems, CAB International, Wallingford, UK, 1996, pp. 137–158.

[24] Laca E.A., Ortega I.M., Integrating foraging mechanisms across spatial and temporal scales, in: West N.E. (Ed.), Rangelands in a Sustainable Biosphere, Proceedings of the Vth International

Rangeland Congress, Society for Range Management, Denver, CO, 1996, Vol. 2, pp. 129–132.

[25] Olton D.S., Handelmann G.E., Walker J.A., Spatial memory and food searching strategies, in: Kamil A.C., Sargent T.D. (Eds.), Foraging Behavior: Ecological, Ethological, and Psychological Approaches, Garland STPM Press, New York & London, 1981, pp. 333–354.

[26] Parsons A.J., Carrère P., Schwinning S., Dynamics of heterogeneity in a grazed sward, in: Lemaire G., Hodgson J., de Moraes A., Nabinger C., de F. Carvalho P.C. (Eds.), Grassland Ecophysiology and Grazing Ecology, CAB International, Wallingford, UK, 2000, pp. 289–315.

[27] Parsons A.J., Thornley J.H.M., Newman J.A., Penning P.D., A mechanistic model of some physical determinants of intake rate and diet selection in a two species temperate grassland sward, Funct. Ecol. 8 (1994) 187–204.

[28] Prache S., Damasceno J., Béchet G., Preferences of sheep grazing down conterminal monocultures of *Lolium perenne – Festuca arundinacea*: test of an energy intake-rate maximization hypothesis, in: Durand J.L., Emile J.C., Huyghe C., Lemaire G. (Eds.), Multi-Function Grasslands – Quality Forages, Animal Products and Landscapes, Proceedings of the 19th General Meeting of the European Grassland Federation, La Rochelle, France, 2002, pp. 258–259.

[29] Ritchie M.E., Scale-dependent foraging and patch choice in fractal environments, Evol. Ecol. 12 (1998) 309–330.

[30] Rodway-Dyer S.J., Cook J.E., Rook A.J., Effect of resource density on the use of spatial memory by foraging sheep, in: Proceedings of the Annual Meeting of the British Society of Animal Science, British Society of Animal Science, 2001, p. 63.

[31] Sibbald A.M., Hooper R.J., Trade-offs between social behaviour and foraging by sheep in heterogeneous pastures, Behav. Proc. (2002) accepted.

[32] Sibbald A.M., Smith D.J.F., Hooper R.J., Individual differences in sociability and their consequences for foraging behaviour in sheep, in: Proceedings of the Annual Meeting of the British Society of Animal Science, Scarborough, British Society of Animal Science, 2000, p. 129.

[33] Statistical Analysis System, SAS/STAT Guide for personal computers, version 6.11, SAS Institute Inc., Cary, NC, 1989.

[34] Thornley J.H.M., Parsons A.J., Newman J.A., Penning P.D., A cost-benefit model of grazing intake and diet selection in a two-species temperate grassland sward, Funct. Ecol. 8 (1994) 5–16.

[35] Veissier I., Le Neindre P., Trillat G., The use of circadian behaviour to measure adaptation of calves to changes in their environment, Appl. Anim. Behav. Sci. 22 (1989) 1–12.

[36] WallisDeVries M.F., Effects of resource distribution patterns on ungulate foraging behaviour: a modelling approach, For. Ecol. Manage. 88 (1996) 167–177.

[37] WallisDeVries M.F., Laca E.A., Demment M.W., The importance of scale of patchiness for selectivity in grazing herbivores, Oecologia 121 (1999) 355–363.