

Effect of cattle grazing a species-rich mountain pasture under different stocking rates on the dynamics of diet selection and sward structure

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Although stocking rate is a key management variable influencing the structure and composition of pastures, only few studies have simultaneously analysed the seasonal patterns of pasture use by cattle, and the adjustments the animals make to maintain intake of a high-quality diet over the grazing season. Therefore, over a 3-year study, we recorded diet selection, plot use and impact of heifers on sward structure and quality under three different stocking rates (0.6, 1.0 and 1.4 livestock units (LU) per ha) in a species-rich mountain pasture of central France. Measurements were made on three occasions between early June and the end of September each year. Overall, heifers selected for bites dominated by legumes or forbs, and against reproductive grass, whatever the stocking rate or season. Selection for tall mixed ($P < 0.05$), short mixed ($P < 0.05$) and short pure grass bites ($P < 0.01$) was more pronounced in plots grazed at the lowest stocking rate. Although heifers' selection for short patches decreased at the end of the season ($P < 0.001$), they continued to graze previously grazed areas, thus exhibiting a typical 'patch grazing' pattern, with the animals that grazed at the lowest stocking rate tending to better maintain their selection for short patches in September (treatment \times period: $P = 0.078$). Neither diet quality nor individual animal performance were affected by the different stocking rate treatments despite high variability in the quantity and quality of herbage offered and differences in diet selection. However, at the 1.4 LU per ha stocking rate, the quantity of forage available per animal at the end of the season, 0.79 t dry matter (DM) per ha of green leaves with the median of sward height at 4.6 cm, approached levels limiting cattle's ability to compensate for the effects of increasing stocking rate. In plots grazed at 0.6 LU per ha, the total herbage biomass remained higher than 3 t DM per ha with more than 30% of plot area still covered by reproductive grass patches at the end of the grazing season, which in the medium term should affect the botanical composition of these pastures. Sward heterogeneity was high in plots grazed at 1.0 LU per ha, with sufficient herbage availability (1.1 t DM per ha of green leaves) to maintain animal performance, and more than 15% of plot area was kept at a reproductive stage at the end of the grazing season. Hence, it could represent the optimal balance to satisfy both livestock production and conservation management objectives.

Keywords: foraging, global positioning system, grazing intensity, patch grazing, seasons

Introduction

Because of its effects on habitat structure and biodiversity, grazing represents a major tool for conservation management. Stocking rate is a key management variable influencing the structure and composition of pastures. A decrease in stocking rate is assumed to promote plant species diversity due to the resulting sward heterogeneity

and reduced disturbance (Grime, 1979). This has been confirmed by surveys of changes in the botanical composition of pastures following a reduction of management intensity or stocking rates (e.g. Kiehl *et al.*, 1996; Hart and Ashby, 1998; Marriott *et al.*, 2004). However, a very low stocking rate is also assumed to reduce plant diversity as a result of competitive exclusion, where the high productivity of some species dominates plant species that cannot compete for light (Grime, 1979). Across Europe, the biodiversity of species-rich semi-natural pastures has been shown to decline under very low stocking rates or after

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cessation of grazing (e.g. Bakker, 1998; Hellstrom *et al.*, 2003; Pavlí *et al.*, 2005).

Hence, it appears that the biodiversity of permanent pastures will decline under both high and very low stocking rates because of the small number of plant species able to tolerate these two management strategies. Although a number of studies have measured the impact of cattle on permanent pastures grazed at different stocking rates (e.g. Hart and Ashby, 1998; Orr *et al.*, 2001; Gillen and Sims, 2006), only a few analysed seasonal patterns in pasture use (Ash and McIvor, 1998; Kohler *et al.*, 2006) and simultaneously quantified the dietary choices of the animals (Mayer *et al.*, 2003). Yet, many features of the structural heterogeneity of swards are the result of decisions made by grazing herbivores about where and when to place bites (Parsons and Dumont, 2003). At a low stocking rate, cattle grazing leads to the generation of patches differing in forage quality and quantity. This patchiness influences subsequent vegetation with a knock-on effect on animal responses. Cattle have been shown to make a trade-off between intake and diet quality such that their preference for high-quality vegetative regrowths varies according to sward height (Dumont *et al.*, 1995) and grazing season (Ginane *et al.*, 2003; Farruggia *et al.*, 2006). Adler *et al.* (2001) gave the name 'patch grazing' to the process by which herbivores continue to graze previously grazed areas, a process that leads to an increase in the spatial heterogeneity of the vegetation.

We have observed that under a medium stocking rate, cattle grazing species-rich mountain pasture exploited short patches of better quality less intensively than those grazing in mesotrophic swards characterised by low-to-moderate plant species diversity (Dumont *et al.*, 2007). It was however hypothesised that there would be a stronger patch grazing response (as described by Adler *et al.*, 2001) in species-rich pastures if they were grazed at a very low stocking rate. Therefore, during a 3-year period, we recorded diet selection, plot use and impact of grazing on sward structure and quality under three different stocking rates in a species-rich mountain pasture of central France. In order to assess the interactions between sward structure and seasonal patterns of diet selection at the different stocking rates, measurements were made on three occasions between early June and the end of September each year. Our aim was not only to describe dietary choices according to stocking rate and season, but also to analyse how cattle make a trade-off between quality and quantity as forage availability decreases. By monitoring animal performance, we were able to assess the efficiency of these behavioural adjustments in maintaining the intake of a high-quality diet.

Material and methods

Experimental sites and animals

The experiment was conducted in an 80-ha natural mountain pasture in the upland area of central France over three

grazing seasons between spring 2002 and autumn 2004. The site had always been extensively managed, resulting in a high botanical diversity. The pasture itself included 170 different plant species, with a majority of oligotrophic species due to the low soil nutrient status. Three stocking rates were compared: a high stocking rate designed to have nearly all the edible biomass consumed at the end of the grazing season; an intermediate stocking rate designed to induce strong structural heterogeneity in the sward; and a low stocking rate designed to quantify the negative effects of competition for light. In the high stocking rate treatment, seven heifers per plot were continuously grazed over the whole grazing season, giving 1.4 livestock units (LU) per ha stocking rate (1 LU = 600 kg live weight), while five heifers grazed each plot in the intermediate stocking rate treatment (1.0 LU per ha) and only three heifers grazed each plot in the low stocking rate treatment (0.6 LU per ha). Nine 3.6-ha experimental plots were created within this pasture, so that each stocking rate treatment could be replicated three times according to a randomised-block design, with some differences in vegetation communities between the blocks. A total of 45, 18-month-old Charolais heifers were used each year. The animals came from the same farm and had all experienced natural upland grasslands with their mothers at a young age. In winter, they were fed a diet composed of 70% medium-quality mountain pasture hay and 30% concentrate (150 g crude protein per kg dry matter (DM)). During the experimental grazing periods, the animals were not given concentrate. Behavioural observations and sward measurements were made in each plot at three periods during the grazing season (25 May to 15 October): in spring (early June) before flowering of major sward components, in summer (end of July) when sward heterogeneity was expected to be at a maximum and in autumn (end of September) when cumulative treatment effects were expected to be at a maximum.

Sward measurements

In each of the three measurement periods, sward height was measured at 500 random points per plot, and the botanical family (grass, legumes or forbs) and vegetation stage (vegetative, reproductive or dead) were recorded at the first place where a stick contacted the undisturbed sward surface. At each point, it was also recorded whether the plants present at ground level below the sampling point were grazed or not. These last data, after being averaged over the whole plot, were taken as a cumulative measure of the impact of the animals from the start of the grazing season. To further estimate sward heterogeneity, we recorded sward height at 10 cm intervals along a 50-m-long permanent transect in the middle of each plot. Each point was considered to be either short or tall according to whether its height was lower or higher than 7 cm. A patch was then defined as an uninterrupted series of either short or tall recordings. This allowed us to calculate the average number of patches per linear metre; the higher this value, the more heterogeneous the sward.

Herbage biomass was determined by cutting five 0.5 m² (10 cm × 5 m long) strips to ground level in each experimental plot at three-week intervals. A further four 0.09 m² (30 × 30 cm) quadrats were cut to ground level in each plot every month, and subsamples were sorted into green leaves, green stems and dead material, and dried at 85°C in order to estimate the sward's morphological composition. The quality of herbage consumed was evaluated using hand-simulated bite samples taken at monthly intervals throughout the grazing season. Four 100-g fresh herbage samples per plot and sampling date were therefore collected by cutting the top half of the extended sward, as this broadly corresponds to what cattle select (Farruggia *et al.*, 2006). At each date, two of the samples were taken from short patches (lower than 7 cm) and the two others from tall patches (higher than 7 cm regardless of vegetation stage). Samples were dried at 60°C for 48 h and analysed for nitrogen content (LECO combustion method (Northern Analytical Laboratory Inc., Merrimack, NH, USA); Sweeney and Rexroad, 1987), fibre content (neutral detergent fibre, NDF: Van Soest and Wine, 1967) and pepsin–cellulase solubility (Aufrère and Michalet-Doreau, 1983) as a measure of organic matter digestibility (OMD).

Animal measurements

Dietary choices were measured by scan sampling at 5-min intervals of the activity of three animals within each group, with one observation day per plot (i.e. three per treatment) at each period. Animals were observed from dawn to dusk to account for diurnal variations in dietary preferences (Rutter *et al.*, 2004). An animal was considered to be *grazing* when it was biting, chewing or swallowing grass, or when it was walking with its muzzle close to the sward. For each animal recorded as *grazing*, the observer moved as close to the animal as possible without disturbing it in order to record one selected bite. Observers decided beforehand which bite to record once they were close enough to the animal (e.g. the fifth one), in order to avoid bias due to picking the bites that were most clearly visible. This required the animals to be trained to accept the close proximity of an observer during grazing.

Bite types (Table 1) were broadly defined according to their botanical composition (grass, legume or forbs), height (short or tall defined as likely to be a limiting factor to instantaneous intake rate or not, i.e. lower or higher than 7 cm) and vegetation stage (vegetative, reproductive or dead). Between scans, additional measurements (bite rate and step rate for 1 min) were made throughout the day to obtain more information on animal selectivity during grazing bouts. A step was defined as a movement of one front leg. Following on from the definition of *grazing* as outlined above, these recordings were interrupted if the animal made at least three consecutive steps with its head up or stood head-up without chewing grass for more than 3 s. A minimum of 15 daily recordings was targeted for each animal. The ratio of bite rate to step rate gives an indication

of animals' selectivity; the lower this ratio, the more selective the animal (Lazo and Soriguer, 1993).

Faecal nitrogen concentration, which was used as an overall indicator of diet digestibility, was measured using the LECO combustion method (Sweeney and Rexroad, 1987). Samples were collected from the rectum every month for each focal animal. Animals were weighed every month and given a body condition score (Petit and Agabriel, 1993), ranging from 1 (very thin) to 5 (very fat).

ETHOSYS collars (Scheibe *et al.*, 1998) were used to estimate the daily grazing time, as direct observation of the animals was not a feasible option for estimating nocturnal grazing activity. All the animals were therefore recorded over a complete 24-h period, once between the end of June and mid July, i.e. between the first two main measurement periods when sward was both abundant and of high quality, and once again between the end of September and mid October when herbage quantity and quality had declined. The sum of all 'head down' values of the ETHOSYS collars was taken as an estimate of grazing duration. Global positioning system telemetry collars were used with differential correction (Schlecht *et al.*, 2004) to monitor animal location on the same days. This allowed us to calculate both distance walked daily and the mean inter-individual distance during grazing bouts. For this second variable, we only considered locations of animals spending at least 1 min 'head down' during the 5-min activity count interval of the ETHOSYS recordings.

Diet selection

Diet selection, defined as the proportion of a sward (bite) type in the diet relative to its proportion in the plot, was quantified by calculating selectivity indices (S_i) for each sward component using Jacobs' (1974) modification of Ivlev's electivity index:

$$S_i = (c_i - a_i) / (c_i + a_i - 2c_i a_i),$$

where c_i is the proportion (between 0 and 1) of component i in the diet and a_i is the proportion (between 0 and 1) of component i in the plot. To estimate a_i , we recorded sward characteristics at 10-cm intervals along the 50-m-long permanent transect in the middle of each plot, with two recordings made at each point, i.e. vegetation at first contact and vegetation dominant at ground level. This procedure was preferred to the random stick measurements as two recordings are needed at each point in order to distinguish between pure and mixed potential bites, as described in Table 1. These data were averaged to estimate the relative abundance of each bite type in the sward. For each bite type (c_i), data for individual animals were first aggregated per day and per plot and then linked to the relative abundance of this bite type in the sward.

S_i varies from -1 (never used) to $+1$ (exclusively used), with negative and positive values indicating avoidance and preference, respectively, and 0 indicating that a sward component is used in proportion to its availability. Jacobs' index was chosen for its low sensitivity to variations in the

Table 1 The different bite types recorded, and the rules used to map transect data to estimates of the bite types available to the animals at that point

Bite types	Bite characteristics	Available bite type (estimated from transect data)
Repro. G	Dominated by green grass stems and ears	(Sward higher than 11 cm with <i>grass stem</i> or <i>grass flower</i> at the upper contact) or (<i>Grass stem</i> or <i>grass flower</i> recorded at both the upper and the lower contacts, whatever the point height) or (<i>Grass stem</i> or <i>grass flower</i> recorded at the upper contact, and <i>legume stem</i> , <i>legume flower</i> , <i>forb stem</i> or <i>forb flower</i> recorded at the lower contact, whatever the point height)
TPG	More than 90% vegetative green grasses higher than 7 cm, i.e. not limiting IIR	(Sward height higher than 7 cm with <i>grass leaf</i> at both the upper and lower contacts) or (Sward height higher than 7 cm with <i>grass leaf</i> at the upper contact, and <i>grass stem</i> , <i>grass flower</i> or <i>grass dead</i> at the lower contact) or (Sward height between 7 and 11 cm with <i>grass stem</i> , <i>grass flower</i> or <i>grass dead</i> at the upper contact and <i>grass leaf</i> at the lower contact)
TMG	Higher than 7 cm, i.e. not limiting IIR, contains some legumes or forbs but dominated by green vegetative grasses	(Sward height higher than 7 cm with <i>grass leaf</i> at the upper contact and <i>legume leaf</i> , <i>forb leaf</i> , <i>legume stem</i> , <i>forb stem</i> , <i>legume flower</i> or <i>forb flower</i> at the lower contact) or (Sward height between 7 and 11 cm with <i>grass stem</i> , <i>grass flower</i> or <i>grass dead</i> at the upper contact and <i>legume leaf</i> or <i>forb leaf</i> at the lower contact)
SPG	More than 90% green vegetative grasses lower than 7 cm, i.e. limiting IIR	(Sward height lower than 7 cm with <i>grass leaf</i> at both the upper and lower contacts) or (Sward height lower than 7 cm with <i>grass leaf</i> at the upper contact, and <i>grass stem</i> , <i>grass flower</i> or <i>grass dead</i> at the lower contact) or (Sward height lower than 7 cm with <i>grass stem</i> , <i>grass flower</i> or <i>grass dead</i> at the upper contact and <i>grass leaf</i> at the lower contact)
SMG	Lower than 7 cm, i.e. limiting IIR, contains some legumes or forbs but dominated by green vegetative grasses	(Sward height lower than 7 cm with <i>grass leaf</i> at the upper contact and <i>legume leaf</i> , <i>forb leaf</i> , <i>legume stem</i> , <i>forb stem</i> , <i>legume flower</i> or <i>forb flower</i> at the lower contact) or (Sward height lower than 7 cm with <i>grass stem</i> , <i>grass flower</i> or <i>grass dead</i> at the upper contact and <i>legume leaf</i> or <i>forb leaf</i> at the lower contact)
L	Dominated by legumes	<i>Legume leaf</i> , <i>legume stem</i> or <i>legume flower</i> at the upper contact, whatever the contact height
F	Dominated by forbs	(<i>Forb leaf</i> spp. at the upper contact, whatever the height) or (<i>Forb stem</i> at the upper contact whatever the height and <i>forb leaf</i> or <i>forb stem</i> at the lower contact)
DG	Dominated by DGs	(Sward height higher than 11 cm with <i>grass dead</i> at the upper contact) or (<i>Grass dead</i> at the upper contact and <i>grass stem</i> , <i>grass flower</i> , <i>grass dead</i> , <i>legume dead</i> or <i>forb dead</i> at the lower contact) or (Sward height lower than 11 cm with <i>grass stem</i> or <i>grass flower</i> at the upper contact and <i>grass dead</i> , <i>legume dead</i> or <i>forb dead</i> at the lower contact)
DF	Dominated by DFs	(<i>Forb dead</i> at the upper contact) or (<i>Forb stem</i> at the upper contact and <i>forb dead</i> at the lower contact)

Repro. G = reproductive grass; TPG = tall pure grass; TMG = tall mixed grass; SPG = short pure grass; SMG = short mixed grass; L = legume; F = forb; DG = dead grass; DF = dead forb; IIR = instantaneous intake rate.

relative abundance of plant components, thus making it possible to rank both abundant and rare plant components according to their acceptability to the animals. Jacobs' selection indices were also calculated for four synthetic patch types. Bites made on both reproductive and dead grass were combined into a single type. Tall pure grass was defined as outlined in Table 1. Tall mixed patches were defined as the sum of tall mixed grass bites with half of the bites made on forbs. Short patches were defined as the sum of short pure grass, short mixed grass and legume bites with half of the bites made on forbs.

Statistical analyses

Data were analysed using the PROC MIXED procedure of the Statistical Analysis Systems Institute (SAS software package, 1999) for repeated measurements in order to account

for observations made in the same plots over three successive periods and three successive years (Littell *et al.*, 1998). Plot was taken as the statistical unit. Jacobs' indices, ingestive behaviour, herbage biomass, structure and quality, and animal performance measurements were analysed in a model including the main effects of treatment, block, year and period, and the interactions treatment \times block, treatment \times year, treatment \times period and period \times year. Differences between treatments were investigated using the Tukey correction for multiple comparisons. Significance of selection for ($S_i > 0$) or against ($S_i < 0$) each vegetation item was determined by comparing the Jacobs' index results to zero using a Student's *t*-test.

We used the same model to assess the effects of treatment, period and the interaction treatment \times period on the proportion of plot area grazed by the animals, estimated from random stick measurements. A Student's *t*-test for

paired data was then used to carry out season-based comparisons between the proportion of plot area grazed by groups of three or five heifers with 3/7 or 5/7 of the proportion grazed by groups of seven heifers. Finally, we used the PROC REG procedure of the SAS software package (1999) to investigate correlations between daily grazing time, distance walked daily or mean inter-individual distance during grazing bouts, and herbage biomass or herbage green leaf mass. This last variable made it possible to combine the quality and quantity of herbage available to the animals.

Results

Herbage biomass and quality, sward structure

Despite strong annual variations ($P < 0.001$), total herbage biomass was systematically higher ($P < 0.05$) in plots grazed at a low stocking rate over the grazing season (Figure 1a). Herbage biomass was also higher in plots grazed at an intermediate compared with a high stocking

rate from the end of July (Figure 1a). Available biomass was reduced at the end of the grazing season ($P < 0.001$). There was a significant treatment \times period interaction ($P < 0.01$), which results from the stability of herbage biomass over the grazing season in plots grazed at a low stocking rate ($P = 0.38$) whereas it decreased between July and September in plots grazed at an intermediate or a high stocking rate ($P < 0.05$; Figure 1a). Similar patterns were observed for green leaf biomass (treatment: $P < 0.001$; period: $P < 0.001$; treatment \times period: $P < 0.05$; Figure 1b), the only differences being that green leaf biomass also decreased at the end of grazing season in plot grazed at a low stocking rate ($P < 0.05$), and that in September it was similar in plots grazed at an intermediate and at a high stocking rate ($P = 0.19$).

The evolution of sward height followed similar trends (Figure 1c), and this regardless of the year (treatment: $P < 0.01$; year: $P = 0.24$; treatment \times year: $P = 0.96$). The median of sward height was lesser in plots grazed at a high stocking rate ($P < 0.01$) compared with the other two treatments, which did not differ ($P = 0.24$). It gradually

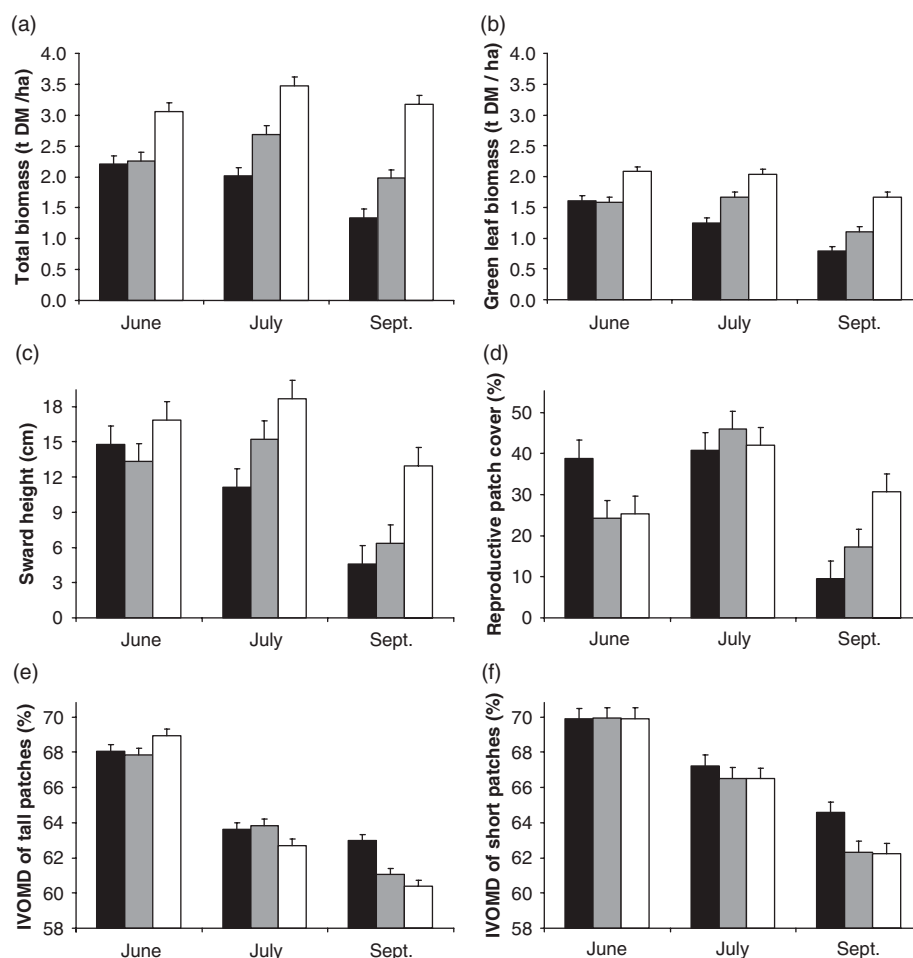


Figure 1 Evolution of herbage biomass and quality over the grazing season in the three stocking rate treatments: (a) total herbage biomass, (b) green leaf biomass, (c) median of sward height, (d) proportion of plot area covered by reproductive patches, (e) digestibility of herbage selected in tall patches and (f) digestibility of herbage selected in short patches. Different shadings are for stocking rate treatments, i.e. black for the high stocking rate, grey for the intermediate stocking rate and open for the low stocking rate.

decreased over the grazing season in plots grazed at a high stocking rate, whereas in plots grazed at an intermediate or a low stocking rate, it was stable between June and the end of July before decreasing by the end of September (period: $P < 0.001$; treatment \times period: $P < 0.01$). The proportion of plot area covered by reproductive patches (estimated from random stick measurements; Figure 1d) was highest in July and lowest in September (period: $P < 0.001$), with little variation of this proportion over the grazing season in plots grazed at a low stocking rate ($P = 0.07$ for June *v.* July; $P = 0.47$ for July *v.* September) and a consistent ranking of the three stocking rate treatments at the end of the grazing season ($P < 0.05$; treatment \times period: $P < 0.001$).

The quality of selected herbage (estimated from hand-simulated bite samples) declined over the grazing season, as indicated by the gradual decrease in the OMD of herbage selected in both the short and tall patches over the grazing season (period: $P < 0.001$; Figure 1e and f). The nitrogen content of selected herbage (whatever the patch type) declined between June and July before rising again in September (28.5, 21.0 and 25.5 g N per kg DM, respectively; $P < 0.001$). The fibre content of herbage selected within short patches increased at the end of the grazing season: 495, 482 and 513 g NDF per kg DM in June, July and September ($P < 0.001$) *v.* 566 g NDF per kg DM on average for tall patches. Conversely, the quality of selected herbage was only slightly affected by stocking rate, even if the quality of herbage selected in the tall patches was higher in plots grazed at a high stocking rate compared with the two other treatments at the end of the grazing season (treatment: $P < 0.05$; treatment \times period: $P < 0.001$; Figure 1e). A similar trend was observed for the quality of herbage selected in the short patches (treatment: $P = 0.10$; treatment \times period: $P = 0.31$; Figure 1f). Overall, significant treatment \times period interactions for several herbage biomass and quality variables confirm that the cumulative treatment effects were at a maximum at the end of the grazing season.

The proportion of plot area that was grazed by the animals, i.e. their cumulative impact from the start of the grazing season, increased over the grazing season ($P < 0.001$) as well as with the stocking rate treatments ($P < 0.001$; treatment \times period: $P < 0.10$; Figure 2a). The proportion of plot area grazed by the animals was directly proportional to the number of animals in the plot in June ($P = 0.48$ for 5 *v.* 7 heifers; $P = 0.33$ for 3 *v.* 7) and July ($P = 0.53$ for 5 *v.* 7; $P = 0.29$ for 3 *v.* 7). In September, animals grazing at a low or intermediate stocking rate had exploited proportionally more area than those grazing at the high stocking rate ($P < 0.001$).

Sward heterogeneity, estimated from the calculation of the average number of patches per linear metre (Figure 2b), was lesser in plots grazed at a low stocking rate ($P < 0.01$), and increased over the grazing season ($P < 0.001$) whatever the stocking rate treatment (treatment \times period: $P = 0.69$).

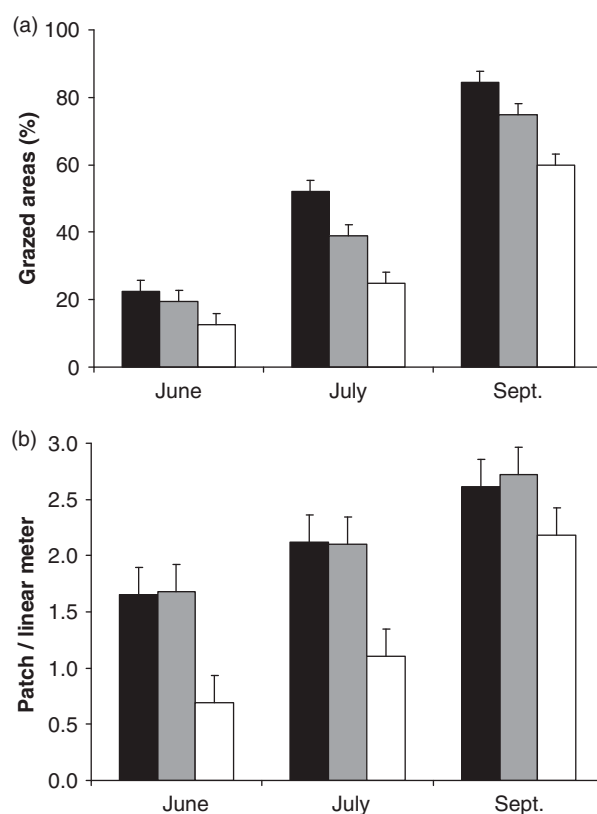


Figure 2 Plot use by the animals according to stocking rate and season: (a) proportion of plot area grazed by the animals, i.e. the cumulative impact of the animals from the start of the grazing season and (b) sward heterogeneity, estimated from the calculation of the average number of patches lower or higher than 7 cm per linear metre. Different shadings are for stocking rate treatments, i.e. black for the high stocking rate, grey for the intermediate stocking rate and open for the low stocking rate.

Diet selection and foraging behaviour

Overall, heifers selected for bites dominated by legumes or forbs, and against reproductive grass, dead grass and dead forbs, whatever the stocking rate or season (Table 2). Over the whole grazing season, heifers increased their selection for tall grass patches (either pure or mixed; $P < 0.001$; Figure 3) and decreased their selection for short grass patches ($P < 0.001$), even though short mixed grass bites were still preferentially selected in September (Table 2). While selection for tall pure grass bites was unaffected by stocking rate, that for tall mixed ($P < 0.05$), short mixed ($P < 0.05$) and short pure grass bites ($P < 0.01$) was more pronounced in plots grazed at a low stocking rate (Table 2). Consequently, with all short vegetation items taken together, selection for these short patches decreased over the grazing season ($P < 0.001$; Figure 3), but the animals grazing at the lowest stocking rate tended to better maintain their selection for short patches in September (treatment \times period: $P = 0.078$; Figure 3). In addition, selection against reproductive grass tended to be less pronounced at the high stocking rate ($P = 0.10$) and in September ($P = 0.086$), although the treatment \times period interaction remained non-significant (Table 2; $P = 0.44$ for reproductive and dead grass taken together: Figure 3).

Table 2 Diet selection and foraging behaviour (BR, GT, Dist., SR, B/S and IID) of heifers according to stocking rate and season

	Stocking rate					Season					Stocking rate × season	
	High	Intermediate	Low	s.e.	Significance	June	July	Sept	s.e.	Significance		
Jacobs' indices												
Repro. G†	-0.49	-0.72	-0.70	0.09	t	-0.79	-0.69	-0.43	0.08	t	NS	
TPG†	+0.12	+0.08	+0.12	0.04	NS	-0.03 ^x	+0.16 ^y	+0.20 ^y	0.04	***	NS	
TMG†	+0.17 ^a	+0.21 ^{ab}	+0.32 ^b	0.04	*	-0.19 ^x	+0.48 ^y	+0.42 ^y	0.05	***	*	
SPG†	+0.17 ^a	+0.12 ^a	+0.42 ^b	0.06	**	+0.46 ^x	+0.25 ^y	-0.00 ^z	0.05	***	NS	
SMG†	+0.43 ^a	+0.47 ^{ab}	+0.65 ^b	0.06	*	+0.65 ^x	+0.57 ^x	+0.33 ^y	0.05	***	NS	
L†	+0.51	+0.30	+0.30	0.12	NS	+0.71 ^x	+0.25 ^y	+0.15 ^y	0.10	***	NS	
F†	+0.19	+0.21	+0.16	0.08	NS	+0.18	+0.14	+0.23	0.06	NS	NS	
DG†	-0.82	-0.84	-0.89	0.04	NS	-0.85	-0.83	-0.87	0.05	NS	NS	
DF†	-0.89	-0.93	-0.82	0.18	NS	-0.68 ^x	-0.98 ^y	-0.98 ^y	0.11	**	*	
Faecal N (g/kg DM)	24.5	24.8	25.1	0.2	NS	29.3 ^x	23.5 ^y	21.7 ^z	0.3	***	NS	
Foraging behaviour												
BR (per min)	56.7 ^a	54.5 ^a	50.7 ^b	0.9	**	51.2 ^x	51.6 ^x	59.2 ^y	0.8	***	NS	
GT (min)	507 ^a	499 ^{ab}	480 ^b	6	*	468 ^x		523 ^y	8	**	NS	
Dist. (m/day)	4670	4410	4140	250	NS	4730 ^x		4090 ^y	170	**	t	
SR (per min)	6.5	6.6	6.7	0.2	NS	7.2 ^x	6.6 ^y	5.9 ^z	0.2	***	NS	
B/S	9.2 ^a	8.5 ^{ab}	7.7 ^b	0.2	**	7.2 ^x	7.9 ^y	10.4 ^z	0.2	***	**	
IID (m)	22.9	22.8	19.6	3.4	NS	18.2 ^x		25.3 ^y	2.1	***	NS	

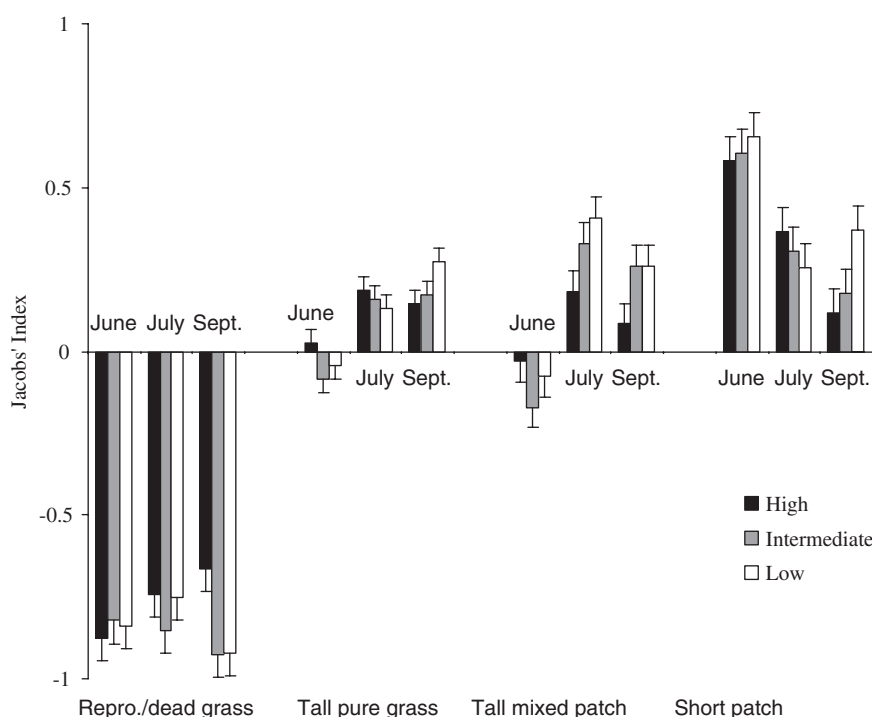
BR = biting rate; GT = daily grazing time; Dist. = distance walked daily; SR = step rate; B/S = bite per step; IID = inter-individual distance during grazing bouts; Repro. G = reproductive grass; TPG = tall pure grass; TMG = tall mixed grass; SPG = short pure grass; SMG = short mixed grass; L = legume; F = forb; DG = dead grass; DF = dead forb; DM = dry matter; NS = not significant; t = $P < 0.10$.

^{a,b}Values within line with different superscript are significantly different at $P < 0.05$.

^{x,y,z}Values within line with different superscript are significantly different at $P < 0.05$.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

[†]Bite types are defined in Table 1. Bold characters indicate for items selected for and italics indicate items avoided.

**Figure 3** Selection for or against reproductive/dead grass, tall pure grass, tall mixed and short patches according to stocking rate and season.

In line with these bite selection measurements and with measurements made on the chemical composition of selected herbage, the nitrogen concentration of faeces, which was used as a synthetic index of diet quality, decreased over the grazing season ($P < 0.001$; Table 2). There was no other significant effect of the stocking rate treatments ($P = 0.33$), and no treatment \times period interaction ($P = 0.99$).

Mean bite rate increased with increasing stocking rate ($P < 0.01$; Table 2), and was also higher in September compared with June and July ($P < 0.001$). Daily grazing time was affected by both stocking rate ($P < 0.05$) and season ($P < 0.01$), without any treatment \times season interaction (Table 2). There was a negative correlation between herbage biomass (HM in t DM per ha) and daily grazing time (GT in min), with $GT = -18.3 \text{ HM} + 548$; $r^2 = 0.22$; $P < 0.01$, although green leaf allowance (GLM in t DM per ha) proved an even better predictor of daily grazing time:

$$GT = -30.6 \text{ GLM} + 553; r^2 = 0.34; P = 0.001.$$

The distance walked daily by the animals was independent of stocking rate ($P = 0.55$; Table 2). On average, animals walked longer distances in June–July than in September ($P = 0.01$). This late-season decrease in distance walked by the animals was only observed at the two higher stocking rates, i.e. $+0.15$ v. -1.16 and -0.92 km/day for the low, intermediate and high stocking rates, respectively (treatment \times period: $P = 0.058$). Step rate during a grazing bout also decreased over the grazing season ($P < 0.001$; Table 2). Together with the increase in biting rate, this resulted in an increase in the number of bites per step in September ($P < 0.001$), which was more pronounced in plots grazed at a high stocking rate, i.e. 9.0, 10.1 and 12.0 bites per step for the low, intermediate and high stocking rates, respectively (treatment \times period: $P < 0.01$).

Stocking rate (and consequently group size) had no effect on mean inter-individual distance (IID in m) during a grazing bout ($P = 0.79$). IID increased at the end of the grazing season ($P < 0.001$; treatment \times period: $P = 0.45$), in line with the negative correlation between herbage biomass (HM in t DM per ha) and IID, with $IID = -3.17 \text{ HM} + 30.89$; $r^2 = 0.21$; $P < 0.01$. Again, green leaf allowance (GLM in t DM per ha) proved an even better predictor of IID:

$$IID = -4.90 \text{ GLM} + 31.01; r^2 = 0.27; P = 0.001.$$

Animal performance

Average daily live-weight gain (LWG) of the animals declined between June and the end of July, before increasing again by the end of September (period: $P < 0.001$; Figure 4a). Conversely, LWG was not affected by the different stocking rate treatments ($P = 0.24$; treatment \times period: $P = 0.36$). Body condition scores gradually increased between June and the end of September (period: $P < 0.001$; Figure 4b), independent of the stocking rate treatments (treatment: $P = 0.84$; treatment \times period: $P = 0.57$).

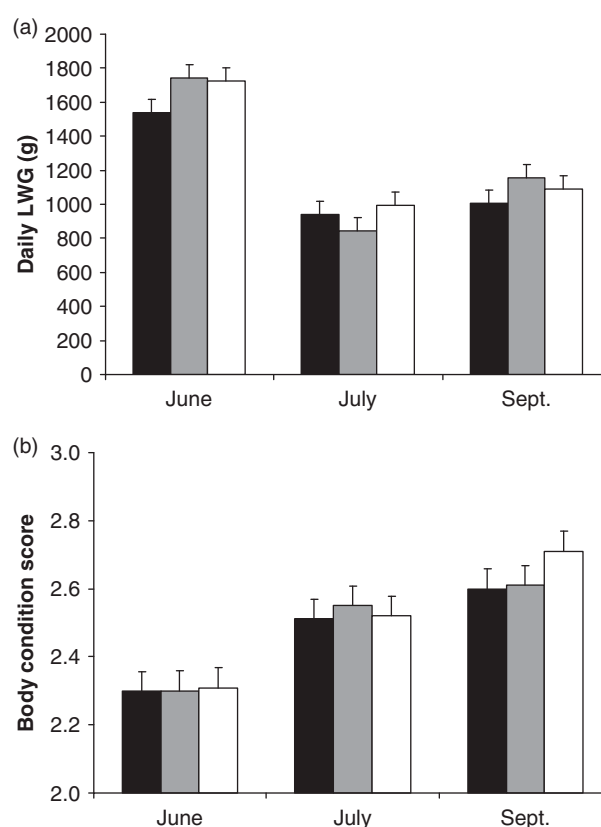


Figure 4 Animal performance according to stocking rate and season: (a) live-weight gain and (b) body condition score. Different shadings are for stocking rate treatments, i.e. black for the high stocking rate, grey for the intermediate stocking rate and open for the low stocking rate.

Discussion

Heifers exhibited very typical selection patterns, selecting for legumes and forbs and against reproductive grass and dead material (Rutter *et al.*, 2004; Dumont *et al.*, 1995 and 2007), whatever the stocking rate or season. They also selected short vegetative patches rather than tall ones due to the higher nutritive value of these short patches (see also McNaughton, 1984). The heifers selected short patches right from the start of the grazing season, regardless of the stocking rate. Although this selection for short patches decreased at the end of the season, the animals continued to graze previously grazed areas, i.e. they showed patch grazing as described by Adler *et al.* (2001). Ewes have also been observed to select short areas from the end of spring and continue to avoid tall areas at the end of the grazing season in a cocksfoot plot grazed at a low stocking rate (Garcia *et al.*, 2004). In a direct comparison that took place in four mesotrophic or semi-natural grasslands across western Europe, Dumont *et al.* (2007) reported that cattle and sheep showed more-pronounced selection of well-grazed areas of better quality in productive mesotrophic vegetations than in semi-natural grasslands with a strong fine-scale heterogeneity and a relatively high nutritive value. However, the authors hypothesised that a more pronounced patch grazing response could occur in

semi-natural grasslands if they were grazed at a lower stocking rate, which is confirmed by our observation that heifers grazing at the lowest stocking rate tended to better maintain their selection for short patches at the end of the season.

The greater exploitation of well-grazed areas of better quality is expected to reinforce the spatial heterogeneity of vegetation over the grazing season. The proportion of plot area that was grazed by the animals, i.e. their cumulative impact from the start of the grazing season, was directly proportional to stocking rate until July, whereas at the end of the season animals grazing at a low or intermediate stocking rate had exploited proportionally more area than those grazing at a high stocking rate. Thus, although cattle grazing at the lowest stocking rate displayed patch grazing until the end of the grazing season, they thus also markedly extended the proportion of plot area kept at a vegetative stage. This 'upkeep' of pastures at the end of the grazing season could contribute to maintaining the sward's agronomic potential in plots grazed at a low stocking rate while limiting the negative effects on biodiversity exerted by the competition for light. However, total herbage biomass remained higher than 3 t DM per ha over the whole grazing season. More than 30% of plot area were still covered by reproductive grass patches at the end of the grazing season, and the balance between short and tall areas (i.e. lower or higher than 7 cm) remained lesser compared with that in plots grazed at a higher stocking rate, which in the medium term should affect the botanical composition of these pastures.

In plots grazed at the intermediate stocking rate, the selection for tall mixed and for short patches that was maintained until the end of the grazing season suggests that animals kept the possibility of grazing areas with high fodder potential (Kohler *et al.*, 2006). Total herbage biomass averaged 2 t DM per ha at the end of the grazing season including 1.1 t DM per ha of green leaves, which is sufficient to maintain animal performance. Sward heterogeneity was systematically higher than that in plots grazed at a low stocking rate, with more than 15% of plot area kept at a reproductive stage at the end of the grazing season. This patch mosaic is expected to favour vegetation and insect diversity by providing resources for species characteristic of short as well as tall vegetation, with reduced disturbance for plant species that are less tolerant to grazing (Grime, 1979; Marriott *et al.*, 2004), and increased habitat quality for insects requiring buffered microclimates (Wallis De Vries *et al.*, 2007). Hence, it could represent the optimal balance to satisfy both livestock production and conservation management objectives.

In plots grazed at the high stocking rate, the proportion of grazed patches reached an average of 85% of plot area at the end of the grazing season. The balance between short and tall areas was similar to that in the plots grazed at an intermediate stocking rate, but herbage availability was strongly reduced at the end of the grazing season with only 1.34 t DM per ha of total herbage biomass (including

0.79 t DM per ha of green leaves) and the median of sward height at 4.6 cm. In September, less than 10% of plot area was kept at a vegetative stage. As these plots became depleted, the heifers were forced to use less-preferred vegetation, resulting in a more balanced selection pattern (see also Kohler *et al.*, 2006). They were less reluctant to feed on reproductive grass, but the animals' consumption of tall patches could have been limited by the presence of faeces or unpalatable plant species such as thistles (see also Cid and Brizuela, 1998). Furthermore, overgrazing of short patches could in the long-term result in divergent vegetation dynamics compared with plots grazed at a lower stocking rate.

When faced with constraints in the quality and availability of pastures, grazing herbivores show great behavioural flexibility to compensate for this restricted forage availability (Iason *et al.*, 1999; Garcia *et al.*, 2003). Late in the season, heifers increased their daily grazing time and inter-individual distance while grazing, which are classical adjustments by which grazing herbivores respond to a decrease in forage availability (Arnold and Dudzinski, 1978). Dumont and Boissy (2000) have observed that in sheep grazed in groups of up to seven individuals, a conflict arose between the motivation to express a food preference and to maintain social contact, animals shifting between the two attractants as the size of their group varied. Here, heifers grazed in groups between three and seven animals did not alter their inter-individual distance, which suggests that compared with sheep the grazing behaviour of cattle could be less influenced by their social context.

Heifers grazing at a high stocking rate increased not only their daily grazing time but also their biting rate and number of bites per step. The increase in biting rate is the mechanistic reaction by which herbivores respond to a decrease in sward surface height (Arnold and Dudzinski, 1978). Heifers grazing at a high stocking rate benefited from a slightly higher quality of selected herbage in both the short and tall patches at the end of the grazing season. In September, they also more strongly increased their bite-to-step ratio compared with the animals grazing at lower stocking rates. This indicates that their initial tactic of research was gradually abandoned in favour of a 'lawnmower'-type tactic (see Roguet *et al.*, 1998 and Garcia *et al.*, 2003, for similar conclusions on grazing sheep). Hence, both their daily distance covered and average number of steps per minute of grazing were reduced at the end of the season.

In plots grazed at the two lower stocking rates, the heifers maintained their intake of a high-quality diet by selecting tall mixed patches and previously grazed short areas. Daily distance walked and bite-to-step ratio remained relatively constant over the grazing season for animals grazing at a low stocking rate, which suggests they kept on exploring the plots in autumn. This is consistent with previous observations that extensively grazed sheep (Garcia *et al.*, 2003) and cattle (Kohler *et al.*, 2006) maintain their selective effort late in the season after the proportion of

reproductive and senescent material in the sward had increased. Consistently, neither diet quality nor individual animal performance was affected by being grazed at a low stocking rate. This observation that quality of cattle diet is quite independent of stocking rate has already been reported under a wide range of sward conditions (e.g. Ortega *et al.*, 1997; Schlegel *et al.*, 2000; Mayer *et al.*, 2003). In addition, our results confirm the flexibility in utilisation of species-rich mountain pastures, in which cattle can adjust their grazing behaviour to maintain intake of a high-quality diet despite high variability in the quantity and quality of herbage offered and differences in diet selection. However, at the 1.4 LU per ha stocking rate, the quantity of forage available at the end of the season could approach levels limiting cattle's ability to compensate for the effects of increasing stocking rate. Conversely, a stocking rate of 1.0 LU per ha would represent the optimal balance to satisfy both livestock production and conservation management objectives in species-rich mountain pastures.

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