Foraging behaviour and occupation pattern of beef cows on a heterogeneous pasture in the Swiss Alps

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ABSTRACT: In the Alps, many summer pastures are under-used due to the decreasing number of livestock. Optimizing the grazing management of heterogeneous pastures implies a better understanding of foraging habits of cattle. The aim of this study was to precise the relationships between cattle behaviour and the characteristics of the vegetation. The experiment was carried out on a pasture encroached by shrubs (mainly *Alnus viridis*) and composed of four contrasted vegetation units at 1800 m a.s.l. Four beef cows were monitored in a paddock of 2.9 ha by Differential Global Positioning System (DGPS) during three rotations, in order to analyze the spatial and temporal occupation pattern. The open grasslands and, to a lesser extent, the tall herb community were significantly more visited than expected if cattle had foraged at random. The shrubby areas were far less visited than expected at random. The monitoring also revealed differences across rotations. Vegetation surveys were also performed to determine the specific contribution and the grazing frequency of the encountered plant species. The most eaten herbaceous plants were not necessarily those known to be the most palatable, even if graminoids were more selected than other plants. *Leontodon hispidus*, *Agrostis capillaris*, *Festuca rubra*, and *Luzula sylvatica* were the most selected species, whereas *Veratrum album* and *Trollius europaeus* were completely avoided. The consumed forage was of better quality than the forage collected at random and its nutrient content showed less variability and remained more constant over the three rotations. The results highlight that the selection processes exerted by cattle are important. They occur at different levels (species, vegetation type, in time) and confirm that an integrative approach is necessary for improving the understanding of cattle foraging behaviour in heterogeneous mountain pastures.

Keywords: subalpine grassland; Global Positioning System; grazing behaviour; herbage selection; mountain pasture; encroachment

Mountain summer pastures are recognized for the many ecosystem services they provide (Millennium Ecosystem Assessment, 2005). In particular, semi-natural grasslands on the alpine and subalpine belt harbour high species richness and therefore play an important role in maintaining biodiversity (Nösberger et al., 1994; Marriott et al., 2004; Kampmann et al., 2008). However, for several decades, the number of livestock grazing on alpine summer pastures has been diminishing, threatening the conservation of such areas through processes of shrub encroachment and natural succession into forests or woodlands (Tasser and Tappeiner, 2002; Freléchoux et al., 2007). Today, one of the main concerns in the Alps relates to the use of wide pasture surfaces with ever-decreasing number of livestock. A better understanding of animal foraging behaviour is necessary for optimization of the use of the pasture resource, as well as the upkeep of the natural value and ecosystem services of mountain summer pastures.

Foraging behaviour, diet selection, and forage intake of domestic herbivores are major processes influencing vegetation dynamics and structure

(McNaughton, 1979; Armstrong, 1996) and are therefore of importance for both animals and grassland management. Many studies have tried to explain these processes by means of experimental observations (e.g. Bailey, 1995; WallisDeVries et al., 1999; Dumont et al., 2002) or by using mechanistic models (e.g. Parsons et al., 1994b; Baumont et al., 2004). However, processes linked to grazing selection are still difficult to predict, especially within heterogeneous environments (Bailey et al., 1998; Prache et al., 1998).

Within heterogeneous pastures, the perception and the use of forage resource by herbivores do not necessarily coincide with vegetation or phytosociological units. Due to their complexity, the plant-animal interactions have to be globally tackled by considering the various processes occurring at different spatial and temporal scales (Parsons and Dumont, 2003). It is largely admitted that an integrative approach, linking optimal foraging theory (Charnov, 1976), landscape ecology, and hierarchy theory is necessary for a better understanding of the foraging processes. The hierarchical models combine several ecological levels, whose boundaries and scales are defined by corresponding animal behaviours (Senft et al., 1987; Senft, 1989; Bailey et al., 1996).

Selection processes can occur at different spatial levels that are characterized by their own time scale (Fortin et al., 2003). In a fenced heterogeneous pasture, the movements of large grazing herbivores are strongly influenced by landscape features, such as slope or distance to water (Bailey et al., 1996), and the large scale mosaic of vegetation (Senft et al., 1987). At smaller spatial levels (patch and feeding station), selective grazing is influenced by the botanical composition (i.e. the abundance of the preferred species) and the nutritive value of the plants (Dumont et al., 2000). Qualitative and structural factors, such as nutrient content, digestibility, and morphology of the plants interact in the choices of the animals (Illius et al., 1992; Parsons et al., 1994a) and their behaviour (Stejskalová et al., 2013). The scale of patchiness as well as its spatial arrangement are other determinants of the selection processes (WallisDeVries et al., 1999; Dumont et al., 2002). Lastly, social behaviour and cognitive abilities also play an important role in foraging behaviour (Dumont and Boissy, 2000; Hejcman et al., 2008).

The present study focuses on the relationship between cattle foraging behaviour and vegetation in mountain pastures of high conservation value in the Swiss Alps. The aim was to better understand how beef cows use heterogeneous pastures. To achieve this goal, Differential Global Positioning System (DGPS) tracking and measures of plant selection by cattle were conducted. The following questions were addressed: (*i*) What are the spatial and temporal occupation patterns of beef cows in a pasture composed of different vegetation units? (*ii*) Which plant species do beef cows prefer to graze? (*iii*) To what extent does the quality of the consumed forage vary throughout the season and how does it differ from forage on offer?

MATERIAL AND METHODS

Study site, grazing system, and animals. The experiment was conducted in 2006 and 2007 on a mountain summer pasture of 27 ha located in the canton of Valais (Swiss Alps), at 1800 m a.s.l. (46°03'41''N, 7°10'53''W). The annual rainfall is about 1100 mm and the average temperature in July 11°C. The snow cover usually lasts from November to May. The vegetation of the summer pasture includes more than 150 vascular plant species with a majority of oligotrophic species, due to the poor nutrient soil status. A reduction in the stocking rate since 1980 has caused the reforestation of many parts of the pasture, with, in particular, *Larix decidua* on dry sunny slopes and *Alnus viridis* on the northern slopes. Average biomass productivity of the grasslands ranged from 1.2 to 2.0 t DM/ha per year.

The herd was composed of beef cows of the local Hérens breed, including 18 cows with 9 calves. The Hérens cattle are a dual purpose breed, adapted both to the production of milk and meat. This breed is a small-size type especially adapted to steep slopes. A mature cow weighs 480–600 kg, and stands 118–128 cm high at the shoulder. The same cows were monitored during the two observation years. The animals were grazed at an average stocking rate of 0.50 LU/ha (1 LU = 1 Livestock Unit, corresponding to a cow of 650 kg live weight). The animals were managed in a rotational system composed of 8 paddocks. The grazing season usually lasted for 110 days, from the beginning of June to the 20th of September.

All observations presented in this study were made in a 2.9 ha paddock located on the northern slope of which ca. 30% is afforested. This paddock was chosen because open grasslands and half-open grasslands alternate to create a mosaic of vegetation. The herbaceous vegetation was moreover representative of the whole pasture. It has been rotationally grazed two (2006) and three (2007) times a year, representing a total of 15 (2006) and 16 (2007) days utilization. For the DGPS survey, four simplified vegetation types were defined on the basis of geo-referenced botanical surveys (Figure 1). The boundaries of the vegetation units were drawn up with high accuracy since a 25 × 25 m grid of vegetation had been set up (Freléchoux et al., 2007): (1) tall herb community, consisting mainly of nitrophilic species such as *Veratrum album*, *Peucedanum ostruthium,* and *Adenostyles alliariae* (13% of the total surface of the paddock); (2) open grasslands, harbouring species of the *Nardion* and the *Poion alpinae* alliances, such as *Nardus stricta*, *Festuca rubra*, *Anthoxanthum alpinum*, *Poa alpina*, *Leontodon hispidus,* and *Trifolium badium* (20%); (3) half-open grasslands, characterized by 10–40% shrubland and including species such as *Chaerophyllum villarsii*, *Homogyne alpina*, *Phyteuma spicatum,* and *Knautia dipsacifolia* ssp. *dipsacifolia* (36%); (4) shrubby areas largely dominated by *Alnus viridis* (31%).

DGPS tracking. The DGPS tracking was conducted in 2007 during the three grazing periods (rotations) in the experiment paddock: (1) 26th to 29th of June, (2) 19th to 23rd of July, and (3) 30th of August to 3rd of September. Four cows were fitted with a customized DGPS tracking harness (Datel Engineering AG, Emmenbrücke, Switzerland). Following preliminary observations made in 2006, the cows were chosen according to their behavioural characteristics (non-dominating animals and with no particular habits). The measurements were usually recorded in RINEX format, every second, over a period of 4–5 days. When satellite reception was poor, the time span was generally 10 s. The weather was mainly dry and sunny during the three rotations.

After each observation period (rotation), differential corrections using virtual reference stations (VRS) were applied. As a second step, the data were downloaded onto a PC and moving averages consisting of 5 successive measurements of position were calculated. The theoretical accuracy of the readings was ± 1 m. However, due to the forest canopy, the actual precision was about ± 3 m.

The DGPS data were crossed with a map of the four main vegetation units (Figure 1) by means of a geographic information system (GIS) software MapInfo Professional (Version 8.5, 2006).

Lastly, the presence index (PI) was computed in each vegetation unit and for each observation period. PI is defined as the ratio between the occupation time in a vegetation unit and its surface, with occupation time and surface expressed as relative proportions of, respectively, the total time of the DGPS tracking and the total surface of the paddock. PI > 1 indicates that animals spend more time in a vegetation unit than expected with regard to its relative surface area.

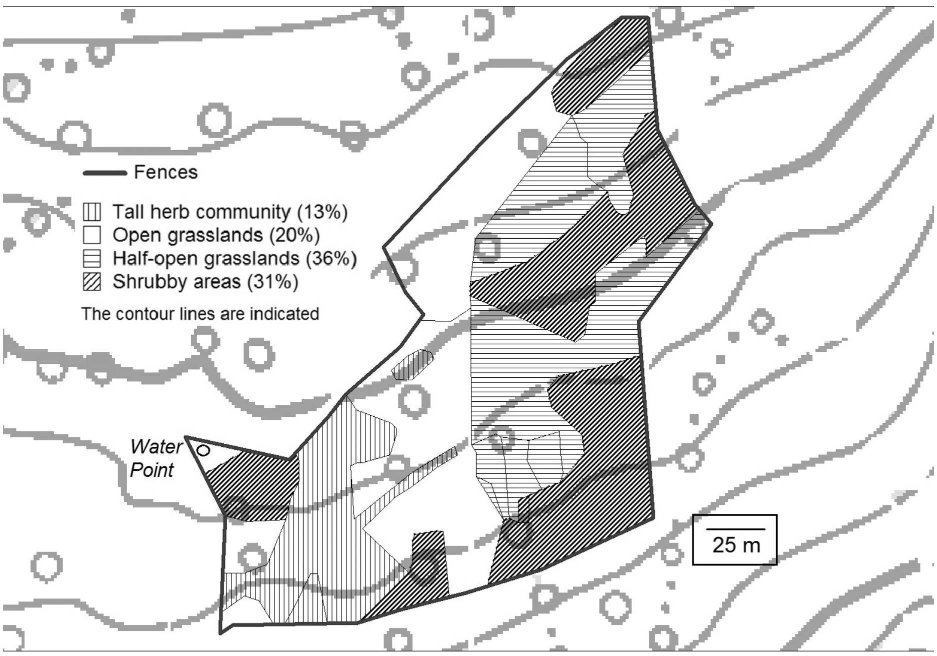

Figure 1. Map of four vegetation units in the experimental paddock grazed by beef cows on a mountain summer pasture

Vegetation survey and plant selection. The species composition in the open parts of the paddock was determined in 2006 according to the point method of Daget and Poissonet (1971), along sixteen transects of 10 m. These botanical analyses were used to assess the selection of herbaceous and heath plants by cattle. The transects were set up among the different vegetation units in places showing a homogeneous vegetation with visible signs of grazing. The sixteen vegetation surveys were made in late June during the first rotation, two or three days after the animals began to graze. The observations, 50 points per transect, were made with a thin metallic bar that was placed vertically every 20 cm along a line of 10 m. At each point, the present species (i.e. those touching the bar) were recorded as "defoliated" or "not defoliated". The plants were considered as eaten as soon as a part of them was missing, independently of the extent of defoliation. A species observed at a point was recorded only once, whatever was its local abundance.

Based on these data, the specific contribution of species i (SC_i) was calculated by dividing the number of presences of species i by the total number of records of all species along the sixteen transects (Daget and Poissonet, 1971). The relative contribution of species i to the total number of defoliated individuals (CD_i) is the ratio between the number of defoliated individuals of species i and the total number of defoliated individuals for all species along all transects. A selection index (SI_i) was defined as CD_i / SC_i for all species that occurred at least twenty times on the sixteen lines. SI > 1 means that the species is consumed in a higher proportion than expected with regard to its specific contribution and reveals selection of this species, whereas SI < 1 would indicate avoidance of this species (Orth et al., 1998).

Nutritive value of consumed and on-offer herbage. During the DGPS tracking, the same four animals were monitored in order to assess the nutritive value of the consumed herbage over the season. During each rotation, pasture herbage was sampled twice: on the first or second day (sampling phase 1) and again on the fourth or fifth day (sampling phase 2) after the beginning of grazing. Three hand-plucked herbage samples were collected for each cow during the three main grazing periods of the day, i.e. between 7.00 and 19.00 h. The collecting time for each sample lasted for about an hour. Picking was carried out according to the procedure described by Berry et al. (2002), which consists in standing very close to the animals (next to the cows' heads) in order to collect the same plant species like those selected by the cows. In this way, it can be assumed that the collected material accurately reflected selected herbage. The three samples of each day were pooled together.

To estimate the quality of the herbage on offer during each rotation, a pool of representative samples (in terms of surface cover and botanical composition) of the different vegetation types and submitted to different intensities of grazing was also collected. These samples were cut by means of electric scissors at a height of about 5 cm. While some samples were collected in areas that were almost never grazed, others were collected in heavily grazed areas.

The samples were oven-dried at 60°C for 72 h and ground through a 1 mm mesh screen. They were analyzed for crude ash (CA), nitrogen (N), neutral detergent fibre (NDF), and acid detergent fibre (ADF) using near-infrared spectroscopy (Büchi NIRFlex N-500; BÜCHI Labortechnik AG, Flawil, Switzerland). Crude protein (CP) was obtained by multiplying N content by 6.25. Organic matter (OM) fraction was determined mathematically considering the difference between dry matter (DM) and CA content. Ten per cent of the analyses were checked by wet chemistry.

Statistical analysis. The statistical analysis of the presence index (PI) values was performed with a Linear Mixed-Effects (LME) model using maximum likelihood procedures (REML). The effects of vegetation unit (Tall herb community, Open grasslands, Half-open grasslands, Shrubby area) and rotation (R1, R2, R3) were set as fixed factors and cow as a random factor. Cow represents the experimental unit ($n = 4$) on which repeated measurements were made. Data were log-transformed prior to analysis to reduce heteroscedasticity.

The first analysis was run with a complete model to test the significance level of the different factors. Then, non-significant terms were successively removed during additional analyses to retain a simplified model (the factors cow and rotation were not significant; there was no correlation between residuals over time). On the basis of the simplified model, an ANOVA was run and confidence intervals were calculated for PI in each combination of rotation × vegetation unit to analyze the deviation of PI values from the null hypothesis PI = 1, while PI = 1 represents the "expected" value, i.e. random cattle occupation of the vegetation units.

In order to test whether cattle exert a selection on the forage they consume, a resampling approach was used. The quality of the consumed forage was compared to the quality expected if cattle had grazed randomly. To simulate foraging at random, 9 999 samples of the same size as the consumed forage samples of the first sampling phase (n = 12) were drawn randomly with replacement from all the samples of the forage on offer (n = 20). By doing this, a null distribution of all possible samples was obtained. Resampling was carried out for each rotation separately, using only data from the first sampling phase. Statistical tests were performed by analyzing the position of consumed forages within the null distribution. The significance of the differences in quality between the consumed forage and the randomly chosen forage samples was then assessed by computing a probability P on the basis of the null distributions, where P represents the proportion of simulated values that are lower (or higher) than the observed value (i.e. the one of the consumed forage).

The variation of the quality of the consumed forage over the season was analyzed using the Mixed-Effects Model of Analysis of Variance. The effects of rotation (R1, R2, R3) and sampling phase (P1, P2) were set as fixed factors and cow as a random factor. Tukey's post-hoc tests were performed to analyze group differences.

All these analyses were performed using R software (Version 2.14.1, 2008) and the nlme package.

RESULTS

DGPS tracking. The vegetation unit had a highly significant effect on the presence indexes (PI), calculated from the DGPS-monitoring data (Figure 2). This effect was affected by the grazing period (significant interaction between rotation and vegetation unit) (Table 1).

Table 1. Effects of fixed factors rotation, vegetation unit and their interaction on presence index. Linear Mixed-Effects model

	DF	F-value	P
Rotation	2; 25	0.85	0.441^{ns}
Vegetation unit	3; 25	28.91	0.0001^{***}
Rotation × vegetation unit	6; 25	2.71	0.036^{*}

DF = degrees of freedom, ns = nonsignificant
$^{*}P < 0.05$, $^{***}P < 0.001$

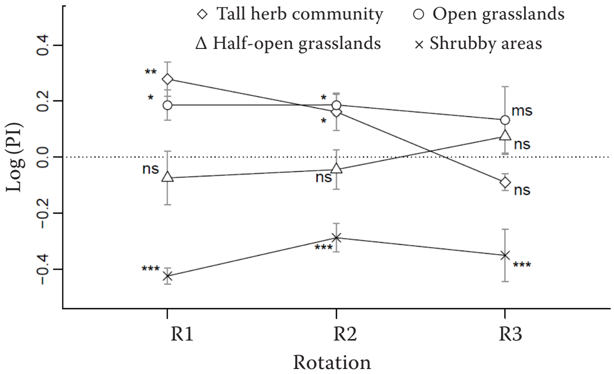

Figure 2. Presence index (PI) of beef cows in different vegetation units during three rotations (R1, R2, and R3) on a mountain summer pasture in 2007

PI values were log-transformed prior to analysis. The zero value corresponds to an occupation time in proportion to the surface of the vegetation unit
levels of significance for the deviation of log(PI) from zero: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$; ms $0.05 < P < 0.10$; ns = nonsignificant (computed from confidence intervals); symbols represent mean values (n = 4) ± SE

The tall herb community was heavily visited early in the season (value of log(PI) significantly higher than 0 during the first and second rotations), whilst during the third rotation, it was visited in proportion to its surface area. During the first and the last rotations, beef cows spent respectively 25 and 11% of their time in this unit which occupied 13% of the total surface.

The PI of the open grasslands remained constantly higher than 1 (i.e. log(PI) > 0) over the whole season, meaning that it was more visited than expected regarding its relative surface. The half-open grasslands were visited in proportion to their surface during the three rotations. The shrubby areas dominated by *Alnus viridis* were the least visited of the four units, with PI values highly significantly lower than expected according to their surface. Cows spent 14% of their time in this unit which occupied 31% of the total area.

Vegetation survey and plant selection. Overall, 92 different plant species were found on the sixteen transects. Selection indexes (SI) were computed for the 23 most abundant species (Table 2). On average, 25% of all the encountered individuals along the 16 transects were grazed plants, comprising 14% of graminoids, 10% of forbs, and 1% of legumes. The most eaten plants were the graminoids: SI > 1 reveals that they were eaten in a higher proportion than their presence (contributing to 38% of the

Table 2. Selection index (SI) of the 23 most abundant (occurrence > 20) plant species on the experimental paddock in the year 2006

	Functional group	All individuals (underfoliated and defoliated)		Defoliated individuals		SI[1]	
		occurrence	specific contribution SC*i* (%)	occurrence	contribution to defoliation CD*i* (%)		
All species		2179	100	552	100		
Graminoids		823	38	305	55	1.46	
Forbs		1123	52	214	39	0.76	
Legumes		163	8	27	5	0.65	
Ligneous plant		70	3	5	1	0.28	
Species with occurrence >20							
Leontodon hispidus	forbs	51	2.3	28	5.1	2.17	SI > *1*
Agrostis capillaris	graminoids	123	5.6	50	9.1	1.60	
Festuca rubra	graminoids	314	14.4	126	22.8	1.58	
Luzula sylvatica	graminoids	125	5.7	47	8.5	1.48	
Anthoxanthum alpinum	graminoids	124	5.7	45	8.2	1.43	
Chaerophyllum villarsii	forbs	160	7.3	58	10.5	1.43	
Poa chaixii	graminoids	36	1.7	12	2.2	1.32	
Nardus stricta	graminoids	28	1.3	9	1.6	1.27	
Plantago alpina	forbs	68	3.1	19	3.4	1.10	
Trifolium pratense	legumes	84	3.9	21	3.8	0.99	SI < *1*
Potentilla aurea	forbs	68	3.1	17	3.1	0.99	
Pulsatilla alp. apiifolia	forbs	24	1.1	5	0.9	0.82	
Alchemilla monticola	forbs	76	3.5	14	2.5	0.73	
Trisetum flavescens	graminoids	26	1.2	4	0.7	0.61	
Soldanella alpina	forbs	21	1.0	3	0.5	0.56	
Geranium sylvaticum	forbs	36	1.7	5	0.9	0.55	
Trifolium repens	legumes	38	1.7	5	0.9	0.52	
Crocus ver. albiflorus	forbs	113	5.2	14	2.5	0.49	
Ranunculus acr. friesianus	forbs	85	3.9	10	1.8	0.46	
Vaccinium myrtillus	ligneous plant	65	3.0	5	0.9	0.30	
Trifolium pallescens	legumes	23	1.1	1	0.2	0.17	
Veratrum album	forbs	28	1.3	1	0.2	0.14	
Trollius europaeus	forbs	59	2.7	2	0.4	0.13	

[1]SI are computed as SC*i*/CD*i*; SI = 1 when the contribution to defoliation of species *i* equals its specific contribution

average vegetation but to 55% of the defoliated plants). Inversely, forbs, legumes, and ligneous plants were consumed in a lower proportion than their relative occurrence would suggest (SI < 1). Considering the species individually, the highest SI were observed for *Leontodon hispidus* (2.2), *Agrostis capillaris* (1.6), *Festuca rubra* (1.6), *Luzula sylvatica* (1.5), *Anthoxanthum alpinum* (1.4), and *Chaerophyllum villarsii* (1.4). Conversely, *Veratrum album* (0.1) and *Trollius europaeus* (0.1) were the least eaten plants. *Nardus stricta* was well eaten (1.3), whereas *Trisetum flavescens* was not (0.6). The SI of the different legume species was found to be relatively low (SI ≤ 1).

Table 3. Differences between the chemical components of the consumed forage and the forage on offer in each rotation (R1, R2, R3) during the first sampling phase (P1), following resampling procedure

	R1		R2		R3	
	deviation[1] |expected – observed|	*P*	deviation |expected – observed|	*P*	deviation |expected – observed|	*P*
DM	1.8	0.024*	1.9	0.073	2.2	0.112
OM	4.1	0.224	3.5	0.337	13.6	0.001**
CP	5.1	0.123	21.7	0.0002***	17.5	0.037*
NDF	5.1	0.562	17.7	0.210	21.4	0.118
ADF	8.3	0.131	10.4	0.163	47.2	0.0002***

[1]deviation is computed as |value expected – value observed| with value expected being the mean of the null distribution for the forage on offer, and value observed corresponding to the value for the consumed forage. *P* values are derived from null distribution

DM = dry matter, OM = organic matter, CP = crude protein, NDF = neutral detergent fibre, ADF = acid detergent fibre

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

Nutritive value of consumed and on offer forage. For one component in the first and second rotation and for three components in the third rotation, the chemical composition of consumed forage was significantly different from that of the forage on offer (Table 3).

The nutritive value of the forage on offer severely diminished over the season with significant increase in ADF and NDF content ($P < 0.05$, multiple pairwise comparison tests) and dispersion of CP and ADF values greatly increased from R1 to R3 (Figure 3).

The nutritive value of the consumed forage remained more constant and showed less dispersion than the forage on offer (Figure 3). Nevertheless, the consumed forage was also significantly affected by the rotation (Table 4), especially for OM, NDF, and ADF contents.

Table 4. Summary of ANOVA for the effects of rotation, sampling phase and their interaction on different chemical components of the consumed forage

		DF	*F*-value	*P*
DM	rotation	2; 15	4.16	0.037*
	phase	1; 15	28.47	0.0001***
	rotation × phase	2; 15	16.88	0.0001***
OM	rotation	2; 15	51.51	0.0001***
	phase	1; 15	0.47	0.504
	rotation × phase	2; 15	0.05	0.947
CP	rotation	2; 15	4.01	0.040*
	phase	1; 15	24.96	0.0002***
	rotation × phase	2; 15	1.72	0.213
NDF	rotation	2; 15	52.38	0.0001***
	phase	1; 15	6.26	0.024*
	rotation × phase	2; 15	5.07	0.021*
ADF	rotation	2; 15	56.71	0.0001***
	phase	1; 15	11.05	0.005**
	rotation × phase	2; 15	9.97	0.002**

DM = dry matter, OM = organic matter, CP = crude protein, NDF = neutral detergent fibre, ADF = acid detergent fibre, DF = degree of freedom

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

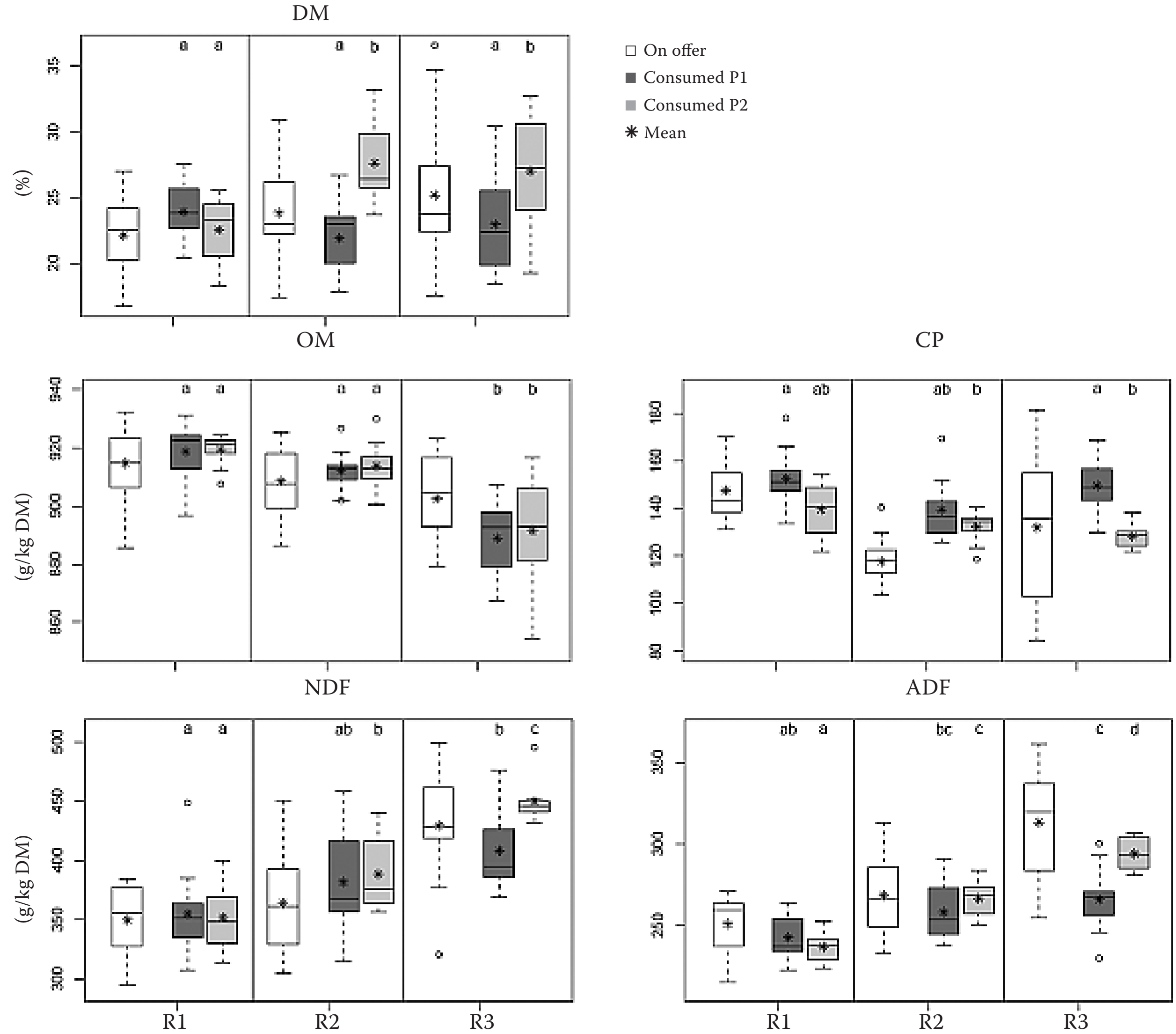

Figure 3. Dry matter (DM), organic matter (OM), crude protein (CP), neutral detergent fibre (NDF), and acid detergent fibre (ADF) contents in the forage on offer (white boxes) and consumed (grey boxes) over three rotations (R1, R2, R3) in the year 2007. The ends of the whiskers represent the lowest datum still within 1.5 interquartile range (IQR) of the lower quartile, and the highest datum still within 1.5 IQR of the upper quartile

[a–d]significant differences ($P < 0.05$) following Tukey's post-hoc test between two sampling phases (P1, P2) and three rotations ($n = 24$)

The consumed forage showed globally higher nutritive value when collected at the beginning of each rotation (first sampling phase) than later during the rotation (Figure 3). The DM content of the consumed forage remained almost constant across the three rotations when considering the first sampling phase, whereas it increased over rotations for the second sampling phase. Similarly, the cell wall components (NDF and ADF) increased over the rotations to a lower extent in the first sampling phase than in the second sampling phase. Finally, the CP content was higher in forage collected in the first sampling phase than in that collected in the second sampling phase.

DISCUSSION

A GPS-based livestock tracking system coupled with GIS information has shown to be a relevant tool in describing the spatial and seasonal grazing patterns of livestock within heterogeneous landscapes (e.g. Boyce et al., 2003; Fortin et al., 2003; Putfarken et al., 2008). In the present study, the combination of this method with observations related to plant selection helped to improve knowledge on foraging behaviour in heterogeneous mountain pastures in the Swiss Alps.

Occupation pattern of different vegetation units. At the paddock scale, animals clearly preferred two vegetation units and several species. Cattle preferentially used the open grasslands (31% of the total time was spent in this unit which represents 20% of the total surface). Open grasslands harbour the presence of many preferred species such as relatively good forage graminoids (*Agrostis capillaris, Festuca rubra*, *Luzula sylvatica*, *Anthoxanthum alpinum*, *Poa chaixii*) and appetent forbs (*Leontodon hispidus*, *Chaerophyllum villarsii*). All these species showed a selection index superior to 1 which proved that cattle actively searched for these species since their consumption was proportionally higher than the proportion of the species in the vegetation. The tall herb community was also heavily visited early in the season, indicating that such areas may also propose attractive forage. However, if the quality of the herbage (i.e. energy content and mineral resources) is one of the major factors influencing foraging patterns across a landscape mosaic (Laca and Demment, 1996; WallisDeVries et al., 1999), the presence of resting places and the proximity of water points may also explain the preferential use of the tall herb vegetation unit (Bailey et al., 1996; Putfarken et al., 2008). Animals showed neither preference nor avoidance for the half open grasslands as this unit was visited in proportion to its surface. On the one hand, the poor herbage quality in this unit, from 10–40% composed of shrubs, may contribute to its non-preference. On the other hand, the non-avoidance may be due to young twigs of small green alder (*Alnus viridis*) which provided a non-negligible resource of a good nutritive value throughout the season (Meisser et al., 2011). As expected, the shrubby area was largely avoided compared to the three other vegetation units. Nevertheless, on average over the entire season, animals spent 14% of their time in this unit. The search for shade or protection against molesting insects during the summer may account for this behaviour.

The DGPS-based livestock tracking also highlighted seasonal variations in the pattern of cattle occupation of vegetation units. The most relevant pattern is the early preference for the tall herb community, which clearly diminished during the season. This underlines the importance of early grazing for ensuring the use of such plant communities. Globally, the expression of spatial preferences was more pronounced early in the season, before tending to more random occupation.

Plant selection. According to WalliesDeVries et al. (1999), selection by large herbivores concentrates on wide-scale patches (plant community, vegetation units) rather than on small ones (feeding stations). However, the present results showed that selectivity can clearly intervene within the plant community.

Globally, graminoids were the most selected plants among the numerous species in the experimental paddock, in consistence with results reported from other studies on semi-natural pastures (Mayer et al., 2003; Sæther et al., 2006; Hessle et al., 2008). This confirms that graminoids constitute a major contribution to the diet of cattle. Surprisingly, the poor digestible grass *Nardus stricta* (i.e. high NDF and low N contents) (Schubiger et al., 1998; Bovolenta et al., 2008) was relatively well consumed. However, vegetation surveys to assess plant selection by cattle took place early in the season when the nutritive value of grasses is still high (Schubiger et al., 1998). This is especially true for *Nardus stricta* which is probably far less consumed one month later.

Forbs were very diversely selected, from highly preferred to completely avoided, for which there may be several explanations. Digestibility is an important factor influencing the selection of forbs, with *Leontodon hispidus*, the most selected species, having a high digestibility (Bovolenta et al., 2008). Also the presence of secondary metabolites or physical factors might have favoured the preference of some species. For example, the high terpenoids content of forbs belonging to the Apiaceae family (Mariaca et al., 1997) could explain the relatively high selection of *Chaerophyllum villarsii.* The abundance (i.e. specific contribution) of species has sometimes been reported to be the main factor explaining their selection by cattle (Agnusdei and Mazzanti, 2001; Carpino et al., 2003). However, present results indicate that in a species-rich grassland, characterized by a low structure of dominance and therefore a high evenness, the abundance of species is not obviously linked to its selection. For species ranging between the abundance of 1–5%, no relationship between specific contribution and contribution to defoliation could be observed.

Finally, the size as well as the spatial pattern of species (e.g. aggregated within large or small patches, loosely distributed) or their vertical arrangement are known to highly influence their selection by animals (Parsons et al., 1994a), almost independently of the species abundance in the vegetation (Dumont et al., 2002). For example, cattle will favour patches where they can maximize the intake rate (Distel et al., 1995). Thus, the absence of selectivity for legumes (SI < 1) may be explained by the small size of *Trifolium repens* and *Trifolium pallescens*, which protected them from selective grazing (Coppa et al., 2011). Another hypothesis could be the fact that cows frequently pull the leaves with the stem. It is thus difficult to estimate properly the consumption of these small species.

Nutritive value of the forage. The composition of the forage on offer showed a broad range of values that became even larger during the season, especially in terms of crude protein and cell wall contents. This reflects the presence of vegetation patches at different vegetative stages, with patches of late vegetative stages (with the highest values of ADF and NDF contents and lowest values of crude proteins) as well as patches in an early vegetative stage with high nutritive value (Bakker et al., 1984). Vegetation patches of high nutritive value may have been maintained in an early vegetative stage through repeated grazing on these patches (Adler et al., 2001), whereas the vegetation which aged with time remained, probably, avoided by animals.

Over the whole season, cattle ingested herbage with higher nutritive value than that on offer. The consumed herbage showed relatively high CP and rather low NDF and ADF contents, corresponding to usual values on alpine pastures (Estermann et al., 2001). As expected for a rather extensive breed, this suggests that the Hérens cows were able to cover their protein and energy requirements, even though the nutritive value of the herbage on offer decreased over the season. The CP content of the consumed forage, which showed almost no variation over the three rotations, reflects selective grazing, which plays an important role in maintaining a sufficient N supply (Berry et al., 2002). Cattle also selected a diet that lowers cell wall contents to compensate fibre increase in the forage on offer during the season. For cell wall content, the deviation between consumed and available herbage was the highest during the last rotation in September. The animals probably maintained the quality of their diet by preferentially visiting the previously grazed patches (Dumont et al., 2007), located in the open and half-open units, through a positive feedback between grazing and herbage quality (Adler et al., 2001).

The crude protein, cell wall, and dry matter contents of selected herbage changed between both sampling periods, especially during the last rotation. This suggests that, within the rotations, the animals first visited the best feeding stations, as similarly reported by Mayer et al. (2003). This again highlights selection processes in such heterogeneous pastures, which are important for animals to be able to meet their energy requirements.

CONCLUSION

By using complementary approaches, this study aimed at improving the knowledge of the utilization of a heterogeneous mountain pasture by beef cows. All approaches highlighted non-random cattle behaviour, reflecting selection processes at different spatial and time levels. Through these processes, cattle can meet their nutritional requirements during the whole grazing season.

The observations of the current study contribute to a better understanding of foraging behaviour and diet selection of beef cows on a subalpine pasture. However, the development of optimal grazing systems in heterogeneous grasslands requires further research, especially about the role that small ruminants and cattle may play against the shrub encroachment phenomenon. In the future, due to a likely continuous declining of the number of cattle, the issue on how to maintain the structural and botanical equilibrium of heterogeneous pastures will become increasingly important.

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REFERENCES

Adler P.B., Raff D.A., Lauenroth W.K. (2001): The effect of grazing on the spatial heterogeneity of vegetation. Oecologia, 128, 465–479.

Agnusdei M.G., Mazzanti A. (2001): Frequency of defoliation of native and naturalized species of the flooding pampas (Argentina). Grass and Forage Science, 56, 344–351.

Armstrong H.M. (1996): The grazing behaviour of large herbivores in the Scottish uplands. Scottish Natural Heritage Information and Advisory Note No. 47. Scottish Natural Heritage, Battleby, UK.

Bailey D.W. (1995): Daily selection of feeding areas by cattle in homogeneous and heterogeneous environments. Applied Animal Behaviour Science, 45, 183–200.

Bailey D.W., Gross J.E., Laca E.A., Rittenhouse L.R., Coughenour M.B., Swift D.M., Sims P.L. (1996): Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management, 49, 386–400.

Bailey D.W., Dumont B., WallisDeVries M.F. (1998): Utilization of heterogeneous grasslands by domestic herbivores: theory to management. Annales de Zootechnie, 47, 321–333.

Bakker J.P., de Leeuw J., van Wieren S.E. (1984): Micropatterns in grassland vegetation created and sustained by sheep-grazing. Plant Ecology, 55, 153–161.

Baumont R., Cohen-Salmon D., Prache S., Sauvant D. (2004): A mechanistic model of intake and grazing behaviour in sheep integrating sward architecture and animal decisions. Animal Feed Science and Technology, 112, 5–28.

Berry N.R., Jewell P.L., Sutter F., Edwards P.J., Kreuzer M. (2002): Selection, intake and excretion of nutrients by Scottish Highland suckler beef cows and calves, and Brown Swiss dairy cows in contrasting alpine grazing systems. Journal of Agricultural Science, 139, 437–453.

Bovolenta S., Spanghero M., Dovier S., Orlandi D., Clementel F. (2008): Chemical composition and net energy content of alpine pasture species during the grazing season. Animal Feed Science and Technology, 140, 164–177.

Boyce M.S., Mao J.S., Merrill E.H., Fortin D., Turner M.G., Fryxell J., Turchin P. (2003): Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience, 10, 421–431.

Carpino S., Licitra G., Van Soest P.J. (2003): Selection of forage species by dairy cattle on complex Sicilian pasture. Animal Feed Science and Technology, 105, 205–214.

Charnov E.L. (1976): Optimal foraging, the marginal value theorem. Theoretical Population Biology, 9, 129–136.

Coppa M., Farruggia A., Pradel P., Lombardi G., Martin B. (2011): An improved grazed class method to estimate species selection and dry matter intake by cows at pasture. Italian Journal of Animal Science, 10, 58–68.

Daget P., Poissonet J. (1971): Une méthode d'analyse phytologique des prairies. Critères d'application. Annales Agronomiques, 22, 5–41.

Distel R.A., Laca E.A., Griggs T.C., Demment M.W. (1995): Patch selection by cattle: maximization of intake rate in horizontally heterogeneous pastures. Applied Animal Behaviour Science, 45, 11–21.

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

Dumont B., Maillard J.F., Petit M. (2000): The effects of the spatial distribution of plant species within the sward on the searching success of sheep when grazing. Grass and Forage Science, 55, 138–145.

Dumont B., Carrère P., D'Hour P. (2002): Foraging in patchy grasslands: diet selection by sheep and cattle is affected by the abundance and spatial distribution of preferred species. Animal Research, 51, 367–381.

Dumont B., Garel J.P., Ginane C., Decuq F., Farruggia A., Pradel P., Rigolot C., Petit M. (2007): Effect of cattle grazing a species-rich mountain pasture under different stocking rates on the dynamics of diet selection and sward structure. Animal, 1, 1042–1052.

Estermann B.L., Wettstein H.R., Sutter F., Kreuzer M. (2001): Nutrient and energy conversion of grass-fed dairy and suckler beef cattle kept indoors and on high altitude pasture. Animal Research, 50, 477–493.

Fortin D., Fryxell J.M., O'Brodovich L., Frandsen D. (2003): Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. Oecologia, 134, 219–227.

Freléchoux F., Meisser M., Gillet F. (2007): Secondary succession and loss in plant diversity following a grazing decrease in a wooded pasture of the central Swiss Alps. Alpine Botany, 117, 37–56.

Hejcman M., Žáková I., Bílek M., Bendová P., Hejcmanová P., Pavlů V., Stránská M. (2008): Sward structure and diet selection after sheep introduction on an abandoned grassland in the Giant Mts., Czech Republic. Biologia, 63, 506–514.

Hessle A., Wissman J., Bertilsson J., Burstedt E. (2008): Effects of breed of cattle and season on diet selection and defoliation of competitive plant species in semi-natural grasslands. Grass and Forage Science, 63, 86–93.

Illius A.W., Clark D.A., Hodgson J. (1992): Discrimination and patch choice by sheep grazing grass-clover swards. Journal of Animal Ecology, 61, 183–184.

Kampmann D., Herzog F., Jeanneret P., Konold W., Peter M., Walter T., Wildi O., Lüscher A. (2008): Mountain grassland biodiversity: impact of site conditions versus management type. Journal for Nature Conservation, 16, 12–25.

Laca E.A., Demment M.W. (1996): Foraging strategies of grazing animals. In: Hodgson J., Illius A.W. (eds): The Ecology and Management of Grazing Systems. 1st Ed. CAB International, Wallingford, UK, 137–158.

Mariaca R.G., Berger T.F.H., Gauch R., Imhof M.I., Jeangros B., Bosset J.O. (1997): Occurrence of volatile mono- and sesquiterpenoids in highland and lowland plant species as possible precursors for flavor compounds in milk and dairy products. Journal of Agricultural and Food Chemistry, 45, 4423–4434.

Marriott C.A., Fothergill M., Jeangros B., Scotton M., Louault F. (2004): Long-term impacts of extensification of grassland management on biodiversity and productivity in upland areas. A review. Agronomie, 24, 447–462.

Mayer A.C., Stöckli V., Huovinen C., Konold W., Estermann B.L., Kreuzer M. (2003): Herbage selection by cattle on sub-alpine wood pastures. Forest Ecology and Management, 181, 39–50.

McNaughton S.J. (1979): Grazing as an optimization process: grass-ungulate relationships in the Serengeti. The American Naturalist, 113, 691–703.

Meisser M., Chassot A., Freléchoux F. (2011): Herbage selection and landscape utilisation by suckler cows on a sub-alpine pasture. In: Proc. 16th Symposium of the European Grassland Federation, Gumpenstein, Austria, 64–66.

Millennium Ecosystem Assessment (2005): Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington, USA.

Nösberger J., Lehmann J., Jeangros B., Dietl W., Kessler P., Bassetti P., Mitchley J. (1994): Grassland production systems and nature conservation. In: T'Mannetje P., Frame J. (eds): Proc. 15th General Meeting of the European Grassland Federation. Wageningen, the Netherlands, 255–265.

Orth D., Carrère P., Lefèvre A., Duquet P., Michelin Y., Josien E., L'Homme G. (1998): L'adjonction de chevaux aux bovins en conditions de sous-chargement modifie-t-elle l'utilisation de la ressource herbagère? Fourrages, 153, 125–138.

Parsons A.J., Dumont B. (2003): Spatial heterogeneity and grazing processes. Animal Research, 52, 161–179.

Parsons A.J., Newman J.A., Penning P.D., Harvey A., Orr R.J. (1994a): Diet preference of sheep: Effects of recent diet, physiological state and species abundance. Journal of Animal Ecology, 63, 465–478.

Parsons A.J., Thornley J.H.M., Newman J., Penning P.D. (1994b): A mechanistic model of some physical determinants of intake rate and diet selection in a two-species temperate grassland sward. Functional Ecology, 8, 187–204.

Prache S., Gordon I.J., Rook A.J. (1998): Foraging behaviour and diet selection in domestic herbivores. Annales de Zootechnie, 47, 335–345.

Putfarken D., Dengler J., Lehmann S., Härdtle W. (2008): Site use of grazing cattle and sheep in a large-scale pasture landscape: A GPS/GIS assessment. Applied Animal Behaviour Science, 111, 54–67.

Sæther N.H., Sickel H., Norderhaug A., Sickel M., Vangen O. (2006): Plant and vegetation preferences for a high and a moderate yielding Norwegian dairy cattle breed grazing semi-natural mountain pastures. Animal Research, 55, 367–387.

Schubiger F.X., Bosshard H.R., Dietl W. (1998): Nährwert von Alpweidepflanzen. Agrarforschung, 5, 285–288.

Senft R.L. (1989): Hierarchical foraging models: effects of stocking and landscape composition on simulated resource use by cattle. Ecological Modelling, 46, 283–303.

Senft R.L., Coughenour M.B., Bailey D.W., Rittenhouse L.R., Sala O.E., Swift D.M. (1987): Large herbivore foraging and ecological hierarchies. BioScience, 37, 789–799.

Stejskalová M., Hejcmanová P., Pavlů V., Hejcman M. (2013): Grazing behavior and performance of beef cattle as a function of sward structure and herbage quality under rotational and continuous stocking on species-rich upland pasture. Animal Science Journal, 84, 622–629.

Tasser E., Tappeiner U. (2002): Impact of land use changes on mountain vegetation. Applied Vegetation Science, 5, 173–184.

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

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