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A herbivore’s food landscape: seasonal dynamics and nutritional implications of diet selection by a red deer population in contrasting Alpine habitats

B. Zweifel-Schielly1*, Y. Leuenberger1, M. Kreuzer2 & W. Suter1

1 Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland
2 ETH Zurich, Institute of Agricultural Sciences, Universitätsstrasse 2, CH-8092 Zurich, Switzerland

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Correspondence
Werner Suter, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland. Tel: +41 44 739 25 67; Fax: +41 44 739 22 15
Email: werner.suter@wsl.ch

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*Current address: Zettess Energy and Environment, Zaunplatz 4, CH-8750 Glarus, Switzerland.

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Abstract
Dietary constraints for large herbivores tend to be most strongly linked to quality of the forage available. In highly seasonal environments, such as mountain areas, both plant quality and available biomass may act as constraints. However, studies addressing the nutritional basis of diet selection of wild large herbivores under harsh conditions in sufficiently large spatial and temporal frameworks are scarce. We studied the functional importance of relative variability in plant quality and biomass for diet selection by a migratory population of Alpine red deer (Cervus elaphus) at the landscape scale and across an annual cycle. Botanical diet composition at plant group level did not show a particular ‘Alpine pattern’ but was similar to known patterns from lowland areas. Sources of variability were season, habitat (either open land or forest) and sex. Red deer foraged selectively in all seasons, and preferences for plant groups were negatively linked to plant abundances. Use and selection of plant groups were associated with high nutritional value (high crude protein and organic matter, low fibre), but partly also with high levels of active tannins. In the cold season, deer made strong nocturnal use of fertilized valley floor meadows offering high-quality grass, but still showed some selection for tannin- and fibre-rich coniferous browse, indicating a need for supplementing grass intake. Altogether, the nutritional value of the diet exceeded that of the forage available in the forested habitat, which was at or below the lower threshold for fulfilling metabolic needs of red deer. High-quality grass on farmed meadows may thus be a critical source of food in mountainous areas during winter.

Introduction
Fulfilling nutritional demands is probably the most basic fitness-relevant task for any animal (Parker, Barboza & Gillingham, 2009). Constraints faced by ruminant herbivores are mainly linked to forage quality (Drent & Prins, 1987; Illius & Gordon, 1992) because green plants provide a relatively small yield of nutrients yet require complicated mechanisms of fibre digestion based on microbial fermentation (Van Soest, 1994). Long retention times of cell wall particles in the digestive tract, in conjunction with a given gut capacity, limit the amount of biomass that can be processed per unit of time, and set a lower limit to tolerable forage quality (Illius & Gordon, 1992; Hanley, 1997). Selecting forage of high protein and low fibre content will not only optimize nutrient and energy intake but also reduce retention time, thus increasing intake capacity (Van Soest, 1994; Mysterud et al., 2001). Additional selection criteria may respond to the need to balance diet for other minerals and for low concentrations of secondary metabolites (Cassini, 1994).

Understanding foraging behaviour requires a scale-dependent view as animals make decisions at various levels of spatial hierarchy (Senft et al., 1987; Bowyer & Kie, 2006; Zweifel-Schielly et al., 2009). Both available plant biomass and plant quality are subject to strong variability in areas with marked seasonal climate, and the need for selective foraging should thus entail responses on more than one spatial scale. Research has mostly focused on the ends of the scale range. At the lower end, with respect to both space and time, decisions taken on a feeding patch (feeding station) are generally well understood (Searle, Hobbs & Shipley, 2005), although much of the work has been performed on domestic species in their specific man-controlled environments (Kyriazakis, Tolkamp & Emmans, 1999). At the upper end of the scale range, behavioural patterns in response to regional inequalities in forage biomass and quality have also received considerable attention,
particularly where ungulates engage in migratory movements to track optimal resources (Fryxell, Greet & Sinclair, 1988; Albon & Langvatn, 1992; Hebblewhite, Merrir & McDermid, 2008). In between these two extremes, however, efficient foraging requires landscape-level strategies that define much of the day-to-day animal-resource interactions. These strategies are not as predictable as those expressed on the smallest scale because behaviours reflect trade-offs between nutritional requirements and other variables, particularly constraints set by man or predators (Parker, 2003; Godvik et al., 2009; Christianson & Creel, 2010). Strategies must be responsive to the spatial resource variability encountered at the landscape scale, and to resource dynamics at a temporal scale integrating changes within and between seasons. Few attempts have been made to functionally link different components of resource use by large herbivores within a spatial and temporal framework large enough to accommodate a population over a full cycle of seasons.

We studied the functional importance of the variability in forage quantity and quality available for diet selection by a migratory population of Alpine red deer (Cervus elaphus) at the landscape scale throughout an annual cycle. Alpine landscapes are typically rugged, offering strong spatial and temporal variability in foraging conditions that may include severe bottlenecks during the snow-rich cold season. Such landscapes should put particular pressure on ungulates to track sufficiently nutritious feeding resources. We have already shown that the migratory movements during the growing season follow a pattern conforming to the forage maturation hypothesis (Zweifel-Schielly et al., 2009). Our aims here are (1) to analyse whether the overall diet pattern of a red deer population living in a harsh Alpine environment is characteristically distinct from the general pattern established in less demanding environments; (2) to identify responses in diet choice and selectivity to pronounced seasonality; (3) to assess the nutritional benefits of the feeding choices observed, in particular of switches between farmland and natural habitats. We hypothesized that (1) red deer should show marked dietary adaptations to strong Alpine seasonality; (2) selection should strongly focus on forage quality (high crude protein and low lignified fibre contents, low concentrations of adverse secondary compounds); (3) the resulting diet should reflect the highest nutrient gain possible from the feeding habitats available.

Materials and methods

Study area

The study area was a 250 km² rugged landscape with steep slopes in the northern Alps near Glarus, east-central Switzerland (47°00′, 09°07′), at elevations from 470 to 2060 m. It comprised the eastern side of an 8-km stretch of a main valley (Linth River) and the entire watershed of a tributary (Sernft River, c. 25 km long) and was thus naturally delineated. The climate is mixed oceanic and continental, with mean annual temperatures between 8°C on the valley floor and 3°C at 1600 m; annual sums of precipitation are c. 1500 mm. Apart from a few small settlements on the valley bottom, land cover roughly consists of one-third each of grassland, forest and rocky areas. The grassland is found in the valley bottom and along lower slopes (10% of the study area), where it is intensively farmed (meadows cut and fertilized on average four times a year), and as alpine pastures above the timberline (25%). Forest covers the slopes in a zonated pattern of deciduous (mostly beech Fagus silvatica; 400–900 m), mixed (beech, silver fir Abies alba and Norway spruce Picea abies; 900–1400 m) and coniferous forest (mainly Norway spruce; 1400–1900 m), and is fringed with subalpine scrubland in places. Structurally, it is mostly a small-scale mosaic of different age classes and canopy closures with frequent small clear-cuts and natural openings, such as wind-throw areas and stream gullies, interspersed with sparsely vegetated rocky areas and cliffs.

Red deer and their spatial routine

The study area encompassed the year-round spatial system of the red deer population in the watershed, with 15 of the animals being GPS collared (seven females, eight males). Most of the deer were migratory and spent the winter at the foot of the slopes around the main valley. In spring, they migrated up the tributary valley and established summer home ranges at various altitudes on the forested slopes, while a few hinds remained near the wintering grounds. Summer densities of red deer in the wider area are estimated at three to four individuals/km² of forested landscape (see Zweifel-Schielly et al., 2009 for more details and data sources).

Diet composition

We studied diet composition by microhistological analysis of epidermal fragments in faeces. Faecal heaps were collected along straight transect lines in the home ranges of the 15 GPS-collared red deer in winter (January–March), spring (May–June), summer (July–September) and autumn (October–November) 2002/2003. A home range was defined as the area used by a collared deer during the 2 weeks prior to pellet sampling. Where home ranges overlapped, transect lines were placed in the non-overlapping part. Still, we did not assign faeces to individual deer because not all deer were marked but used the information on the possible sex of the dung producer (see below). The procedure also ensured that we sampled diet across the population. For each faecal heap, we recorded whether it was found in forest or open land.

We collected all fresh heaps found but considered only the five most evenly spaced heaps per transect. Ten pellets were analysed from each heap. The resulting sample size (winter n = 70, spring n = 75, summer n = 65, autumn n = 65) varied slightly between seasons according to the number of occupied home ranges. The pellets were oven-dried at 60°C for 48 h to constant weight, and their weights and lengths measured. Faecal pellet size in red deer is known to depend on body size, and males produce larger pellets than females (Mitchell & McCowan, 1981). We compared measurements of pellets from male and female home ranges, and although we could not
exclude that a given faecal heap originated from an animal other than the home range owner, we found pellets in winter to be on average larger in male-owned home ranges (mean dry weight ‘male’: 0.55 g, ‘female’: 0.36 g; t_{\text{length}} = 5.598, d.f. = 67, \(P < 0.001\); t_{\text{weight}} = 3.275, d.f. = 67, \(P = 0.002\)). In spring and summer, the difference was not significant (mean dry weight ‘male’: 0.42 g, ‘female’: 0.39 g), and there was also none in autumn when the home ranges widely overlapped during rutting. Since pellet lengths and weights were highly correlated (\(r = 0.708, P < 0.001\)), we used only weight as an indication of sex and classified pellets \(>0.4\) g as male and pellets \(\leq 0.4\) g as female (or young of either sex).

Microhistological analysis of the faeces followed the procedure described in Suter et al. (2004). Fragments were identified according to eight plant groups: graminoids, forbs (including Rubus spp.), dwarf shrubs (mainly Vaccinium sp.), ferns, mosses, deciduous browse (trees and shrubs), coniferous browse (mainly Picea abies) and unidentified. Our reference material included 85 plant species common in the study area and originating from all eight plant groups.

Microhistological analysis may produce biased results because digestion affects epidermal cells differently, depending on cell wall thickness and diet composition. Graminoids tend to be overestimated relative to forbs by some 30%, but the rank order of ingested plant groups often remains unaffected (Holechek, Vavra & Pieper, 1982; McInnis, Vavra & Krueger, 1983; Bartolomé et al., 1995). We compared diet compositions established from faeces and from rumen contents of 24 red deer collected in the same area in autumns 2000–2003. Assuming that the rumen analysis revealed the true diet better (although some bias may occur also in rumens), graminoids were in fact overestimated, and forbs underestimated in the faeces. Other plant groups did not significantly differ between the two analyses, as the 95% confidence intervals of the respective proportions were widely overlapping. The rank order of the plant groups was the same for faeces and rumen contents. In most analyses, we therefore used ranks instead of absolute proportions of plant groups for comparing diet with forage biomass and quality on offer. Some approaches required absolute proportions that were calculated in two ways, with uncorrected proportions and with proportions of graminoids reduced by 30%, and forbs increased by 30% (see above). Results were only weakly affected and in no case the direction of selectivity (for or against a food type, see Table 2) changed. Therefore, we report only uncorrected results.

**Forage biomass and quality**

We assessed available quantity and nutritional value of forage by analysing living plant biomass from 30 sampling plots (9 m² each) drawn randomly from farmed grassland on the valley floor and from 65 plots (400 m² each) on the forested slopes. We considered living plant biomass up to a height of 1.70 m to be available to red deer. It was harvested on four systematically selected subplots (forest: 1 m², meadows 0.09 m²) in spring (May–June), summer (July–August) and autumn/winter (October–November) 2001 in a way so that each subplot site was cut only once. The smaller subplot size on meadows was considered sufficient as these meadows are structurally homogeneous and uniform in species composition, containing few grasses (e.g., Dactylis glomerata, Poa pratensis, Festuca rubra, Lolium perenne and Agropyron repens) and very few forbs only. The plant material from the forest was sorted into the same groups as used in the diet analysis (without class ‘unidentified’), but in each group, the biomass of the four subplots was pooled for later analysis. For ‘coniferous browse’, we sampled only the latest annual shoots because browsing marks suggested that red deer did not normally consume more than the annual increment. ‘Deciduous browse’ was only sparsely present on trees and shrubs in autumn after leaf fall, and we supplemented the necessary material for chemical analyses with shed leaves, but did not measure their biomass available on the ground.

The plant material collected was stored in darkness in a cool container to minimize continued cell respiration. Within a few hours at most, plant biomass was oven-dried at 50°C for 48 h and then cooled, weighed and milled through a 0.75-mm screen. This procedure is among the standard methods for preservation of forages (Tiemann et al., 2009). Forest samples often were pooled by a random procedure to yield enough material for all chemical analyses (hence most sample sizes <65 in Supporting Information). Contents of dry matter and organic matter (dry matter minus total ash) were determined with a TGA-500 furnace (Leco Instruments, St Joseph, MI, USA) at steps of 105 and 550°C, respectively. Nitrogen contents were measured with a CN-2000 analyzer (Leco Instruments, St Joseph, MI, USA), and results multiplied by 6.25 to calculate crude protein contents (Van Soest, 1994).

Protein and (digestible) energy contents in food plants may vary independently across seasons (Alldredge, Peek & Wall, 2002). As digestibility is strongly influenced by thickness and composition (cellulose, lignin) of the plant cell wall (Spalinger, Robbins & Hanley, 1986), the profile of the various fibre fractions is a good indicator of digestibility (Van Soest, 1994). Plant samples were therefore analysed for neutral-detergent fibre (NDF, all fibre fractions combined), acid-detergent fibre (ADF, cellulose and lignin) and acid-detergent lignin (ADL, lignin) with the Fibertec System (Foss Tecator, Höganäs, Sweden). The content of NDF was measured after digestion with \(\alpha\)-amylase (Van Soest, Robertson & Lewis, 1991), while ADF and ADL were determined according to the Association of Analytical Communities (AOAC) International (Cunniff, 1995: no. 973.18 C and D). Hemicellulose and cellulose contents were calculated by subtraction of ADF from NDF, and ADL from ADF, respectively. Samples were corrected for residual ash.

Apart from fibre properties, there are several groups of plant secondary compounds that may influence palatability and digestibility of protein and cell walls, and tannins probably are the most important group among them (Van Soest, 1994). For this reason, we analysed protein-binding capacity by tannins (tannin activity) in 25 randomly drawn samples of deciduous browse and 5 samples of the other plant groups. The material was separated from the collected plant biomass before drying and was frozen instead in a plastic bag and then freeze-dried (following Tiemann et al., 2009, for...
Nutritional implications of diet selection by red deer

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Tannin analysis followed methods 1 (extraction of tannins) and 3 (determination of protein-precipitation capacity, bovine serum albumin-dye method) as outlined in Makkar & Goodchild (1996). Measurement of the protein-binding assay was preferred to analysis of total phenolic content, as the latter comprises a mixture of differently active compounds and does not always correlate with protein-binding activity (Stadler Martin & Martin, 1982). However, one must be aware that a tiny fraction of the protein-binding capacity may be due to compounds other than tannins (for instance, the values for graminoids and mosses that do not contain tannins are slightly >0, though not significantly different from 0; Supporting Information).

While red deer can graze ground vegetation under snow of up to 30 cm high, cutting plant biomass under snow present in mid-late winter (January–March) was not feasible. For comparing winter diet with available forage, we used the forage data from autumn that were obtained in October–November because it can reasonably be assumed that at least relative biomasses and nutritional values remained constant between plant groups after the end of the growing season.

Because faeces and vegetation samples had to be collected in two different years, possible annual variation in plant biomass and quality would have been an issue if responses of plant groups to annual variation in growth conditions had not been proportional. We thus resampled eight of the 65 forest plots and five of the 30 valley floor meadow plots in spring, summer and autumn 2002 and analysed them for crude protein content. We assessed differences in proportions of plant groups (angular transformed) in forest and in crude protein content between years using two-way ANOVA (general linear model) with factor ‘plant group’ and a repeated measurement on factor ‘year’. While year of sampling did not influence proportions of plant groups present in forest, we found crude protein contents to be lower in summer 2002 than in 2001 ($F_{1,25} = 4.484$, $P = 0.044$). However, there was no significant interaction between year and plant group in any season, suggesting that plant growth responses to growth conditions were similar in all plant groups.

**Main statistical analyses**

We used de-trended correspondence analysis (see McGarigal, Cushman & Stafford, 2000 for justification) to identify seasonal, habitat- and sex-related variation in diet composition, and quantified associations between proportions of plant groups and axes scores with Pearson correlations. The influence of the factors ‘season’, ‘habitat’ and ‘weight class of faecal pellets’ (i.e. the substitute for sex) on axes scores 1–4 was tested with a multivariate three-factorial ANOVA (GLM). We omitted the non-significant dependent variable ‘axis 4’ and non-significant interactions for improving the model. Because sample size among groups in the ANOVA was uneven, we used unweighted means and unique (type III) sums of squares. Distribution of residuals was examined with Q-Q-plots and found to be normal in all cases, while graphing variance with Tukey–Anscombe plots showed that assumptions of homogeneity were not violated. Multiple pairwise tests were performed with unweighted means and Bonferroni adjustments.

For comparing diet composition with standing available biomass of the plant groups, we calculated rank preference indices (Johnson, 1980) and made multiple comparisons according to Waller & Duncan (1969). Johnson’s rank analysis is recommended as being relatively robust compared with preference analyses based on proportions (Krebs, 1998).

The available biomass by plant group was calculated for the forested part of the entire study area, that is at the landscape scale; therefore, available biomass values were the same for each faecal sample. We had to exclude the farmed meadows because no meaningful biomass values of grass biomass available could be calculated: first, biomass strongly fluctuated with the harvesting regime, and second, the total area available to deer for grazing depended on the level of human disturbance. Because the graminoids found in the diets could have come from either farmed meadows or forested slopes, the plant group ‘graminoids’ was not included in the analyses involving preference ranks for the plant groups.

We confine the term ‘preference’ to the rank order analyses and use ‘selection’ and ‘avoidance’ of plant groups in accordance with other resource selection studies, that is a food type is selected/avoided when its proportion in the diet is significantly higher/lower than its proportion in the (accessible) vegetation on offer; to be ‘selective’ refers to either way. We applied Spearman correlations to search for associations between the means of preference ranks, proportions of plant groups in diet, proportions of available plant groups in forest and quality of plant groups. For the correlations of diet with forage quality, we used the quality values of graminoids from valley floor meadows rather than from forest, because the collared red deer had spent 37–81% of the nocturnal (feeding) time outside the forests (Zweifel-Schielly et al., 2009). Nutritional value of diet and of forage available in the forest was calculated by multiplying the proportions of plant groups in faeces and on forest plots, respectively, with the seasonal mean values of plant quality. Here, we used two sets of diet quality values, one calculated with the graminoid data from forests and the other from valley floor meadows. Differences between diet and forage were considered significant when their 95% confidence intervals did not overlap.

All analyses (except where specified) were made with statistical software SPSS® (release 11.0.1, SPSS Inc., Chicago, IL, USA) and the software package R (R 2.3.1; R Development Core Team, Vienna, Austria) using $\alpha = 0.05$ as the level of significance.

**Results**

**Overall diet composition of Alpine red deer**

Of the 27 506 epidermal fragments determined in the 275 faecal samples, 675 (2%) could not be assigned to any plant
group and were excluded from the total in all but the correspondence analyses. The resulting diet composition did not depend much on whether fragment number or total fragment area was used to calculate plant group proportions (r > 0.8), thus we report only results based on total fragment area. Overall, graminoids were the main diet component (41%), followed by forbs (18%), coniferous browse (15%) and deciduous browse (14%) (see Table 1 for seasonal values). Other plant groups contributed only minor proportions (dwarf shrubs 6%, ferns 3% and mosses 2%). Despite some identification uncertainty, Rubus spp. very likely made up the majority of the forbs group.

Table 1 Composition of red deer diet and of available forage on the forested slopes [mean proportions (%) and standard deviations], and preference ranks (6 = highest, 1 = lowest, different ranks differ at P ≤ 0.05, Waller–Duncan test, P < 0.001)

<table>
<thead>
<tr>
<th>Plant group</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
<th>Autumn</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diet Rank</td>
<td>Diet</td>
<td>Available</td>
<td>Rank</td>
<td>Diet</td>
</tr>
<tr>
<td>Graminoids</td>
<td>48.5(20.1)</td>
<td>45.2(19.3)</td>
<td>7.7(15.2)</td>
<td>34.1(20.9)</td>
</tr>
<tr>
<td>Forbs</td>
<td>2.6(5.5)</td>
<td>3</td>
<td>20.0(20.3)</td>
<td>34.9(28.6)</td>
</tr>
<tr>
<td>Dwarf shrubs</td>
<td>4.7(6.6)</td>
<td>4</td>
<td>3.9(5.7)</td>
<td>6.2(18.5)</td>
</tr>
<tr>
<td>Ferns</td>
<td>0.6(1.2)</td>
<td>3</td>
<td>1.6(4.3)</td>
<td>4.6(10.5)</td>
</tr>
<tr>
<td>Mosses</td>
<td>3.3(4.2)</td>
<td>1</td>
<td>1.8(2.9)</td>
<td>32.7(32.6)</td>
</tr>
<tr>
<td>Deciduous browse</td>
<td>9.8(8.2)</td>
<td>5</td>
<td>11.6(9.8)</td>
<td>13.0(19.7)</td>
</tr>
<tr>
<td>Coniferous browse</td>
<td>30.6(20.3)</td>
<td>6</td>
<td>15.9(20.6)</td>
<td>0.8(2.5)</td>
</tr>
</tbody>
</table>

Graminoids are not ranked as the diet included graminoids from pastures where no meaningful assessment of availability could be done. Sample sizes: winter diet n = 70, spring diet n = 75, all other n = 65.

Temporal, spatial and sex-specific patterns of diet composition

The first four axes in the correspondence analysis explained 85% of the variance in diet composition. Axis 1 (40% of variance) was positively correlated with coniferous browse (r = 0.910) and negatively with forbs (r = 0.804) and deciduous browse (r = 0.319; Fig. 1). Axis 2 (18% of variance) was positively associated with graminoids (r = 0.940) and negatively with forbs (r = 0.403) and coniferous browse (r = -0.402; Fig. 1). Axis 3 (16% of variance) correlated positively with dwarf shrubs (r = 0.755), deciduous browse (r = 0.536), ferns (r = 0.466) and negatively with forbs (r = -0.426). Axis 4 (11% of variance) was linked to ferns (r = 0.842) and negatively to deciduous browse (r = -0.381). The plant group ‘unidentified’ was located near the centre of the axes, suggesting that unidentified fragments were evenly distributed across plant groups and that their omission from further analyses did not introduce a bias (Fig. 1, upper graph).

Season, habitat (open land or forest) and sex (i.e. weight class of faecal pellets) influenced axes scores in the correspondence analysis as main factors on at least one axis each, and habitat and sex did so additionally in interaction with season. Season explained half of the variance in diet composition (R² = 0.489), while effects of habitat (R² = 0.079), sex (R² = 0.095) and their interactions (R² = 0.202) were weaker but still significant. Diet composition differed among all seasons except between spring and summer (P < 0.05). There was a continuous shift in diet from winter through spring and summer to autumn along axis 1, from more coniferous browse to more forbs and deciduous browse (F1,263 = 42.2, P < 0.001, Fig. 1, Table 1). Additionally, the scores of axis 3 were higher in autumn than in other seasons (F1,263 = 14.1, P < 0.001), that is diet consisted of more dwarf shrubs, deciduous browse and ferns in this season. There was also a tendency for consuming less graminoids in summer and autumn compared with winter and spring (Fig. 1, Table 1).

Effects of habitat and sex on diet composition were significant on their own (habitat axis 1: F1,263 = 7.8, P = 0.006, axis 2: F1,263 = 11.9, P = 0.001, sex axis 1: F1,263 = 12.2, P = 0.001, axis 3: F1,263 = 10.3, P = 0.001), as well as in interaction with season (season × habitat axis 2: F2,263 = 2.7, P = 0.046, season × sex axis 1: F2,263 = 7.5, P < 0.001, axis 2: F2,263 = 2.7, P < 0.049). Faeces from open land contained lower proportions of coniferous browse in spring and summer, and more graminoids in summer than faeces from forest (non-overlapping 95% confidence intervals for axis 1 in spring and for axis 2 in summer; Fig. 2a). Differences relating to sex were only detected in winter when heavier faeces (>0.4 g) contained higher coniferous and lower graminoid proportions than faeces ≤0.4 g (non-overlapping 95% confidence intervals for axis 1 and 2; Fig. 2b). As habitat- and sex-specific variation in diet composition was weak compared with seasonal differences, we investigated diet selection and nutritional consequences only with respect to season.

Diet selection at plant group level

Red deer foraged selectively throughout the year (Table 1). Precisely speaking, graminoids have to be excluded from this statement despite being the most commonly eaten diet component, because availability and thus preference indices for graminoids could not be calculated (see Materials and methods). Seasonal differences in preference ranks were particularly pronounced for coniferous and deciduous browse, ferns and dwarf shrubs (shift by two ranks, Table 1). Coniferous browse was the most preferred group in winter, spring
and summer, deciduous browse in autumn. Preferences for ferns (spring) and dwarf shrubs (summer–autumn) were relatively highest in the growing season, while preferences for forbs and mosses were consistently low throughout the year.

Preferences were not correlated with the proportions of the plant groups in the diet, but were negatively associated with abundance of plant groups in forest in winter, spring and summer ($r = -0.943, P < 0.01$).

![Figure 1](image_url)
Water and crude protein contents in plants generally declined from spring to autumn, whereas contents of cell wall constituents (NDF, ADF, ADL) increased (Supporting Information). The increase was mostly due to cellulose and lignin, whereas hemicellulose contents rather declined. Organic matter contents and tannin activity did not show specific seasonal patterns.

Correlations between mean nutritional parameters of the plant groups and their use or preference were found in all seasons, but selection for groups of high nutritional value (low ADF, low ADL, high crude protein, high organic matter content) occurred almost exclusively during the growing season, with the exception of organic matter in winter (Table 2). Mean crude protein contents and protein/fibre ratios were positively correlated with use in summer but negatively with preference in winter (protein/fibre ratio also in autumn). In summer, we additionally found a positive relationship between preference and mean tannin activity. Among nutritional parameters in plant groups, mean ADF and ADL were negatively correlated with mean crude protein contents in summer ($r = -0.821$, $P \leq 0.023$).

We compared nutritional value of diet and of available forage to test whether red deer selected for elevated nutritional quality of diet at large. Regardless of the origin of graminoids (farmed meadows or forested slopes), throughout the year, the diet contained somewhat more organic matter (+1 to +8%), less ADF (~4 to ~24%) and less ADL (~18 to ~42%) than the forage available in forest (Table 3). Additionally, it included > 25% more active tannins in summer and autumn and more...

**Figure 2** Differences in diet composition of red deer according to faecal samples found in open land or forest in spring and summer (a), and according to weight classes of faecal pellets in winter (b), correspondence analysis. Closed circles: (a) faeces from forest (spring $n=62$, summer $n=53$), (b) faecal pellets $>0.4$ g ($n=34$). Open circles: (a) faeces from open land (spring $n=13$, summer $n=12$), (b) faecal pellets $\leq 0.4$ g ($n=35$). For ordination of plant groups, see Fig. 1.
hemicellulose in most seasons (+12 to +70%, except in autumn) than the forage on offer in the forest.

With respect to crude protein content, diet quality depended on whether the graminoids were taken on the forested slopes or on farmed meadows where their nutritional value was considerably higher (+14% in spring, +38% in summer, +91% in autumn: Supporting Information). Assuming that the graminoid fraction in the diet came from farmland, diet would have had somewhat higher contents of water (+5 to +15%, spring to autumn) and crude protein (+9 to +16%, spring to autumn), and less NDF (−10 to −18%) and cellulose (−6 to −15%) compared with the average forage available in forest. If the graminoids were also obtained in the forest, the diet would have had slightly lower nutritional value than the average available forage in forest (crude protein −11 to −23%, cellulose +5 to +6%), particularly outside the growing season in autumn and winter. This is because graminoids in forest offered less nutritional value than many forest plant groups. The strongest difference was found in winter for crude protein content (Table 3).

**Discussion**

The overall botanical diet composition of red deer showed the normal pattern of a mixed feeder, as graminoids dominated throughout the year and the three next ranking groups, forbs (i.e. mostly *Rubus* spp.), coniferous and deciduous tree browse, each contributed 1.5 to 3 times less. Dominance of

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**Table 2** Correlation coefficients ($r$) between use (mean % in diet) or preference (mean rank, see Table 1) and nutritional parameters (means) of the different plant groups ($n = 7$ for use, with parameter values for graminoids taken from farmed valley floor meadows; $n = 6$ for preference, as graminoids were not ranked)

<table>
<thead>
<tr>
<th></th>
<th>Winter Use</th>
<th>Winter Preference</th>
<th>Spring Use</th>
<th>Spring Preference</th>
<th>Summer Use</th>
<th>Summer Preference</th>
<th>Autumn Use</th>
<th>Autumn Preference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water content</td>
<td>−0.357</td>
<td>−0.771</td>
<td>0.571</td>
<td>0.143</td>
<td>0.643</td>
<td>−0.200</td>
<td>0.571</td>
<td>−0.543</td>
</tr>
<tr>
<td>Organic matter</td>
<td>0.214</td>
<td>0.943*</td>
<td>0.000</td>
<td>0.829*</td>
<td>0.036</td>
<td>0.943*</td>
<td>−0.143</td>
<td>0.714</td>
</tr>
<tr>
<td>Tannin activity</td>
<td>−0.214</td>
<td>0.486</td>
<td>0.214</td>
<td>0.371</td>
<td>0.071</td>
<td>0.943*</td>
<td>−0.214</td>
<td>0.429</td>
</tr>
<tr>
<td>Crude protein</td>
<td>−0.107</td>
<td>−0.886*</td>
<td>0.107</td>
<td>0.143</td>
<td>0.750</td>
<td>−0.371</td>
<td>0.536</td>
<td>−0.600</td>
</tr>
<tr>
<td>NDF content</td>
<td>−0.429</td>
<td>−0.257</td>
<td>−0.571</td>
<td>−0.029</td>
<td>−0.821*</td>
<td>−0.086</td>
<td>0.536</td>
<td>−0.086</td>
</tr>
<tr>
<td>ADF content</td>
<td>−0.536</td>
<td>−0.029</td>
<td>−0.679</td>
<td>−0.486</td>
<td>−0.714</td>
<td>−0.029</td>
<td>0.536</td>
<td>0.086</td>
</tr>
<tr>
<td>ADL content</td>
<td>−0.321</td>
<td>−0.029</td>
<td>−0.750</td>
<td>−0.257</td>
<td>0.543</td>
<td>0.371</td>
<td>0.000</td>
<td>−0.257</td>
</tr>
<tr>
<td>Hemicellulose</td>
<td>0.643</td>
<td>−0.143</td>
<td>0.071</td>
<td>0.543</td>
<td>0.179</td>
<td>0.371</td>
<td>0.000</td>
<td>−0.257</td>
</tr>
<tr>
<td>Cellulose content</td>
<td>−0.500</td>
<td>0.143</td>
<td>−0.357</td>
<td>−0.314</td>
<td>−0.429</td>
<td>−0.371</td>
<td>−0.429</td>
<td>0.086</td>
</tr>
<tr>
<td>Protein/NDF ratio</td>
<td>−0.107</td>
<td>−0.886*</td>
<td>0.250</td>
<td>−0.086</td>
<td>0.679</td>
<td>0.200</td>
<td>0.536</td>
<td>−0.600</td>
</tr>
<tr>
<td>Protein/ADF ratio</td>
<td>−0.107</td>
<td>−0.886*</td>
<td>0.536</td>
<td>−0.029</td>
<td>0.786*</td>
<td>−0.257</td>
<td>0.536</td>
<td>−0.600</td>
</tr>
<tr>
<td>Protein/ADL ratio</td>
<td>−0.036</td>
<td>−0.771</td>
<td>0.536</td>
<td>−0.029</td>
<td>0.786*</td>
<td>−0.257</td>
<td>0.321</td>
<td>−0.829*</td>
</tr>
<tr>
<td>Protein/hemicellulose ratio</td>
<td>−0.536</td>
<td>−0.371</td>
<td>−0.071</td>
<td>−0.257</td>
<td>0.000</td>
<td>−0.429</td>
<td>0.607</td>
<td>−0.029</td>
</tr>
<tr>
<td>Protein/cellulose ratio</td>
<td>0.321</td>
<td>−0.543</td>
<td>−0.143</td>
<td>0.143</td>
<td>0.786*</td>
<td>−0.257</td>
<td>0.607</td>
<td>−0.086</td>
</tr>
</tbody>
</table>

Values in bold: $P < 0.1$, *$P < 0.05$.

NDF, neutral-detergent fibre; ADF, acid-detergent fibre; ADL, acid-detergent lignin.

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**Table 3** Differences (%) of nutritional contents of the diet compared to the forage available in the natural habitat, that is on the forested slopes (measured at plant group level; sample sizes as in Table 1)

<table>
<thead>
<tr>
<th>Contents</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
<th>Autumn</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Forest Meadows</td>
<td>Forest Meadows</td>
<td>Forest Meadows</td>
<td>Forest Meadows</td>
</tr>
<tr>
<td>Water</td>
<td>−12*</td>
<td>−1</td>
<td>+15*</td>
<td>−4*</td>
</tr>
<tr>
<td>Organic matter</td>
<td>+8*</td>
<td>+2*</td>
<td>+6*</td>
<td>+6*</td>
</tr>
<tr>
<td>Tannin activity</td>
<td>+22</td>
<td>+21</td>
<td>−7</td>
<td>+25*</td>
</tr>
<tr>
<td>Crude protein</td>
<td>−23*</td>
<td>+13*</td>
<td>+2</td>
<td>−3</td>
</tr>
<tr>
<td>NDF</td>
<td>+7*</td>
<td>−15*</td>
<td>+6</td>
<td>+3</td>
</tr>
<tr>
<td>ADF</td>
<td>−4*</td>
<td>−19*</td>
<td>−13*</td>
<td>−9*</td>
</tr>
<tr>
<td>ADL</td>
<td>−18*</td>
<td>−24*</td>
<td>−40*</td>
<td>−26*</td>
</tr>
<tr>
<td>Hemicellulose</td>
<td>+47*</td>
<td>+70*</td>
<td>+11*</td>
<td>+51*</td>
</tr>
<tr>
<td>Cellulose</td>
<td>+6*</td>
<td>−15*</td>
<td>+2</td>
<td>+2</td>
</tr>
</tbody>
</table>

Because the graminoids from forested slopes and farmed meadows differed in their contents, two sets of values are given: one calculated with the values for the graminoid fraction in the diet using the content data from forest, and one with the data from farmed meadows.

*95% confidence intervals of diet and available forage did not overlap.

NDF, neutral-detergent fibre; ADF, acid-detergent fibre; ADL, acid-detergent lignin.
grasses/sedges is a recurrent feature of red deer diet across Europe irrespective of area, climate type or altitude, whereas proportions of tree browse and dwarf shrubs can vary strongly with habitat (Gebert & Verheyden-Tixier, 2001; Cook, 2002). Christianson & Creel (2007) came to analogous conclusions in reviewing winter diet studies of elk: graminoids were consistently selected, while browse was consumed according to availability. The mean proportion of 41% graminoids in our study was above the average calculated from European studies (30%), but the overall botanical composition fitted the diet type of mixed-deciduous woodland identified by Gebert & Verheyden-Tixier (2001). The lack of fundamental differences from diet patterns established in more benign climates and topographies suggests that dietary adaptations to harsh environmental conditions must be achieved at a finer level of resolution within the mixed feeder pattern.

We did indeed find that diet composition varied, mostly in response to season and much less to habitat and sex. This is consistent with several regional studies, although in a continental-wide meta-analysis dominated by studies from lowland sites, habitat was found to be more important than season (Gebert & Verheyden-Tixier, 2001). Despite the slight decrease in graminoid proportions found from winter to summer, seasonal variation was mainly an effect of changing proportions of coniferous and deciduous browse that produced a continuous shift in diet composition from winter through spring and summer to autumn, with a switch back from autumn to winter.

Habitat-related variation was found only for spring and summer. Although diet always comprised food originating from open and forested habitats, faeces collected from open land were more strongly grass-dominated than faeces from forest, which in turn contained more coniferous browse. Because the passage time of food in the gut is 50 h and more (Illius & Gordon, 1992; Hummel et al., 2006), droppings do not necessarily represent a meal obtained from the place where the droppings were collected. Habitat-related differences are thus likely to reflect consistent differences between individual deer, probably in the degree to which deer continued to use farmed grassland into spring and summer. In winter, grazing of valley floor meadows at night, supplemented by tree browsing presumably during daytime, had been the common strategy of all red deer (Zweifel-Schielly et al., 2009). Winter, on the other hand, was the only season when slight sex-specific differences in diet composition emerged, as the larger faeces assigned to males contained more coniferous browse and less graminoids than the smaller droppings assigned to females and immatures. Stags have occasionally been found to eat a diet of higher fibre content than hinds in winter (Clutton-Brock, Guinness & Albon, 1982), likely because their larger body size lets them better tolerate food of low nutritional quality (Staines, Crisp & Parish, 1982; Barboza & Bowyer, 2000).

Meeting nutritional requirements can be a difficult task for larger herbivores (Drent & Prins, 1987). Problems generally relate to (1) available food quantity to ensure a sufficient intake rate, and to (2) food quality, which includes several aspects, for example gain of energy and protein, provision of micronutrients, or avoidance of secondary compounds and toxins. While selective foraging is the rule rather than the exception in mammalian herbivores (Cook, 2002), nutritional bottlenecks in highly seasonal environments, such as rugged mountain areas, may pose additional demands on diet choice. Red deer fed selectively throughout the year as the seasonal use of plant groups was not related to plant abundance, and preferences (which however did not include the graminoid category) even showed a negative relationship to abundance in all seasons except autumn. The most strongly preferred plant group (annual shoots of conifers within the reach of deer) was comparatively rare throughout the year, whereas abundant forage tended to be selected against (forbs, mosses). Mosses consistently had the lowest preference rank; in general, they are poorly digestible (Ihl & Barboza, 2007).

Selectivity was mostly but not entirely geared toward plant groups having elevated nutritional value of some sort (lower cellulose/lignin, lower lignin, or higher crude protein contents than in the available forage). During summer, the use of plant groups was positively associated with most parameters indicating elevated nutritional value. Summer was the only season when high contents of crude protein in food plant groups were linked to low contents of indigestible fibre. In the other seasons, no positive associations between use or preference and high protein or low lignin contents emerged, presumably because fibre-rich components were relatively more important in the diet. Relatively high proportions of coniferous browse in winter diet even produced a negative link between preferences and nutritional value of plant groups. However, this may partly be an artefact attributable to the unavoidable omission of graminoids in the calculations. Graminoids were strongly used year-round and generally were of high nutritional value (high contents of crude protein and hemicellulose, low contents of lignin), although graminoid quality diverged between farmed meadows and forested slopes as the year progressed. Quality on the regularly fertilized meadows remained high throughout the year, whereas crude protein contents of graminoids on forested slopes decreased substantially from spring to autumn, and lignin contents nearly doubled. Therefore, farmland grass contained 1.3–2.3 times as much crude protein and 20–80% less lignin than the other plant groups in autumn and winter.

The overall diet selected by red deer was substantially lower in lignin than the biomass on offer, no matter where the grasses were obtained. But to achieve higher diet quality in terms of higher (max. 16%) crude protein and lower (max. 15%) cellulose contents, red deer depended on grazing the farmed meadows during the non-growing season. In summer, deer spent some 75% of their time in the forests (Zweifel-Schielly et al., 2009), and diet (which may have included grasses originating from alpine pastures or open glades in the forest) did not exceed the generally high crude protein contents of the forage available at that time (see also Verheyden-Tixier et al., 2008).

Selectivity with plant groups other than graminoids and mosses, that is avoidance of forbs, selection of dwarf shrubs and tree browse, did not indicate a quest for elevated nutritional value in terms of high protein and low fibre contents.
Therefore, the other selection criteria have to be considered in these cases: avoiding high concentrations of adverse plant secondary compounds or toxins (Cassini, 1994), demand for micronutrients (Van Soest, 1994), mixing diet with fibre to enhance rumen microbial activity (Hobbs et al., 1981), or increasing biomass uptake to reduce grazing time (Bergman et al., 2001). These motives need not be mutually exclusive. Plant secondary compounds may have been a reason for avoiding ferns from summer onwards, as these tend to build up toxic substances (Somvanshi et al., 2006). High concentrations of protein-binding tannins, however, did not seem to provoke avoidance at plant group level, as preferences were positively related to tannin activity in summer, and diet in most seasons contained more bioactive tannins compared with the forage available on the forested slopes. Some avoidance of specific compounds at the level of plant species or even plant parts (Tixier et al., 1997; Clauss et al., 2003; Torregrossa & Dearing, 2009) may have contributed to low preference for forbs, but in general, indifference of ungulates towards active tannins at plant group level is not unknown. Inhibitory effects may be mitigated through the nutritional quality of the tanniniferous plant and its neighbours in the diet (Belovsky & Schmitz, 1994; Villalba, Provenza & Bryant, 2002; Tiemann et al., 2008), and many deer have developed salivary proteins to bind and neutralize tannins (Austin et al., 1989; Hagerman & Robbins, 1993; Duncan & Poppi, 2008). There is even evidence that low levels of tannic acid may improve food conversion efficiency (Clauss et al., 2003).

That said, it seems that the relatively strong consumption of tree browse is better explained by one of the other available motives for selectivity, that is, uptake of micronutrients, fibre or energy. Micronutrients (e.g. minerals, vitamins) have received far less attention than other dietary aspects of wild ungulate herbivory (Duncan & Poppi, 2008), but there is evidence that deciduous and coniferous browse can provide micronutrients which are otherwise limiting (Groot Bruin-derink, Lammertsma & Hazebroek, 2000; Ohlsen & Staaland, 2001; Humann-Ziehank et al., 2008). Other studies which found deer and other wild herbivores to consume more fibre-rich diet than expected explained this either with adaptations in the digestive tract of a mixed feeder who needs to balance protein and fibre ingestion for the benefit of microbial activity (Hobbs et al., 1981; Seccombe-Hett & Turkington, 2008; Christianson & Creel, 2009), or as a means to achieve sufficient biomass intake (Hobbs et al., 1981). In our study, red deer were able to graze the high-quality grass of the valley floor meadows only during night-time when no human disturbance occurred (Zweifel-Schielly et al., 2009). We thus suppose that red deer had a need to browse conifers during their daytime retreat into forests where other forage was sparse, first to achieve sufficient energy intake over 24 h, and, second, to keep microbial rumination processes in pace with the ultradian activity rhythms (Berger et al., 2002).

Our results support the notion that large herbivores living in harsh Alpine conditions focus their spatial strategies on accessing forage of high quality in all seasons. Patterns of migration during the growing season are in agreement with the forage maturation hypothesis (Zweifel-Schielly et al., 2009; see also Hebblewhite et al., 2008). The forage quality data for spring and summer suggest that requirements of red deer are easily met with, including increased needs by lactating hinds or dominant stags for protein (Cook, 2002). However, the data on fibre contents (particularly the elevated lignin contents) show that towards autumn and winter, digestibility of forage available on the forested slopes might have become critical for meeting daily energy requirements necessary to prevent excessive body mass loss (Chen et al., 1998; Christianson & Creel, 2009). For crude protein contents, the lower threshold is given as 8% for adult female elk (Cook, 2002; similar in Van Soest, 1994). Values in forage on the forested slopes were either below or just at that threshold; only Rubus leaves had higher values but were present in low biomass. Obtaining food solely from the forested slopes may thus have been critical to fulfil metabolic requirements in terms of nutrient gains and probably insufficient in terms of energy gains, because accessible biomass of ground vegetation was particularly low during times of deep snow cover (December–February). Grass on the fertilized valley floor meadows, however, contained more than twice the threshold amount of crude protein. Therefore, obtaining about half of the daily ingested biomass in the form of this abundant, highly digestible and protein-rich source must have been the only way to fulfil nutrient requirements.

To our knowledge, this is the first study at the landscape scale to demonstrate that forested natural habitats may be severely limited in their nutritional capacity to sustain red deer through winter. Farmed grassland on the floor and along the lower south-facing slopes of larger valleys are major constituents of red deer wintering grounds in mountainous landscapes over much of temperate Europe, at least where supplementary feeding is not part of the management (e.g. Righetti, 1995; Spitzenberger, 2001). Pastures were also found to be key habitats for nocturnal feeding by red deer in northern latitudes (Godvik et al., 2009), where body weights of red deer increased with the proportion of meadows available at the landscape scale (Mysterud et al., 2002). Enhanced nutritional quality of winter-range habitats can even increase winter survival of deer (Schmidt & Hoi, 2002; Bishop et al., 2009). Therefore, the large-scale maintenance of high grass quality in winter brought by intensified agriculture may have been an underestimated driver of the dramatic increase seen in red deer numbers over much of Europe in the last decades. Browsing and bark-peeling damage is often reported from landscapes where red deer are confined to closed forest in winter. Managers might thus consider improving access for red deer to open farmland in such areas to mitigate impacts on forests.

**Acknowledgements**

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GIS support; to B. Moser for statistical advice and to M. Clauss and an anonymous reviewer for helpful comments on the manuscript. Rumen samples were made available by R. Hauser and game rangers of the Canton of Glarus.

References


### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Seasonal nutritional composition of the plant groups constituting the red deer diet (mean g/100 g dry matter unless stated otherwise, standard deviation (SD) and sample sizes [n]). Sp: Spring, Su: Summer, Au: Autumn.

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