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Authors: Suter, Werner, Suter, Ursula, Kriisi, Bertil, and Schütz, Martin

Source: Wildlife Biology, 10(1) : 43-50

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2004.008

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Spatial variation of summer diet of red deer *Cervus elaphus* in the eastern Swiss Alps

Werner Suter, Ursula Suter, Bertil Krüsi & Martin Schütz

Suter, W., Suter, U., Krüsi, B. & Schütz, M. 2004: Spatial variation of summer diet of red deer *Cervus elaphus* in the eastern Swiss Alps. - Wildl. Biol. 10: 43-50.

By micro-histological analysis of plant remains in faecal pellets, we studied the diet of red deer *Cervus elaphus* during a summer season in the subalpine zone of the Swiss National Park in the eastern Swiss Alps. Hitherto, very little quantitative information on the diet of Alpine red deer populations has been published. Faecal species composition was found to conform to the general pattern known from elsewhere: it was dominated by graminoids with dwarf shrubs (mainly *Erica carnea*) as a strong secondary component and forbs and coniferous browse in minor proportions. Practically all pellet samples contained food obtained both from pastures and forests, irrespectively of where the pellets were collected. Although forest plants contributed 28% of the fragment numbers and 41% of the fragment area in the pellets, coniferous tree browse accounted for only 2.5 and 5.0%, respectively. This supports the findings of other studies that red deer most likely has little impact on the forest dynamics in the Park. The spatial uniformity of faeces composition did not reflect the substantial differences in grassland vegetation between three study areas, probably because deer locally selected nutritious graminoids (particularly red fescue *Festuca rubra*) at patch level.

Key words: Alps, browsing, Cervus elaphus, diet, faecal pellet analysis, grazing, red deer, selectivity, Switzerland

Werner Suter, Bertil Krüsi & Martin Schütz, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland - e-mail addresses: werner.suter@wsl.ch (Werner Suter); bertil.kruesi@wsl.ch (Bertil Krüsi); martin.schuetz@wsl.ch (Martin Schütz)
Ursula Suter, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland, and Natural History Museum Bern, Bernastrasse 15, CH-3005 Bern, Switzerland - e-mail: milonia@gmx.ch*

**Present address: Reussgasse 12, 5620 Bremgarten, Switzerland*

Corresponding author: Werner Suter

Received 18 February 2002, accepted 11 April 2003

Associate Editor: Jean-Michel Gaillard

Red deer *Cervus elaphus* is the most important browsing ungulate species in the subalpine forests in most of the Alps. Its influence on tree regeneration is widely believed to be so strong as to compromise forest rejuvenation (e.g. Motta 1996). In the Swiss National Park, an alpine area where red deer is not managed, fear of detrimental effects caused by deer on forest regeneration has repeatedly been expressed (Kurth, Weidmann & Thommen 1960, Leibundgut & Schlegel 1985). However, recent studies using long-term data sets have concluded that red deer is not able to suppress the establishment of mountain pine *Pinus mugo* seedlings on

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intensely grazed subalpine pastures permanently, nor are browsing ungulates an important factor in driving the dynamics of mountain pine stands (Schütz, Krüsi, Achermann, Moser, Leuzinger & Nievergelt 1999, Krüsi & Moser 2000, Schütz, Krüsi & Edwards 2000).

In general, forest dynamics are extremely complex processes, and the role of ungulates in the long term is usually not well understood beyond general principles (Russell, Zippin & Fowler 2001). Modelling the dynamics of forests under herbivore pressure (e.g., Kienast, Fritschi, Bissegger & Abderhalden 1999) could prove helpful if the models incorporate data on herbivore behaviour. Particularly important will be data on diet selection at plant species level (Hanley 1997).

While the diet composition of red deer has been analysed in detail in many lowland areas of Europe, very few quantitative studies have been published from the Alps. In the Swiss National Park too, impact of ungulate herbivores has so far been mainly based on quantifying signs of browsing shown by the plants in question. Since there are also chamois *Rupicapra rupicapra* and other browsing species present in addition to red deer, such data often do not allow understanding of species specific effects. We therefore studied the diet of red deer in the Swiss National Park during the summer of 2000 by use of micro-histological analysis of plant fragments contained in the faecal pellets, which allowed us to identify the plant species eaten. Our aims were 1) to record the overall pattern of summer diet composition, 2) to quantify the importance of tree browse in the diet, 3) to identify possible temporal and spatial variation in diet composition, and 4) to assess possible species specific selectivity of deer feeding on pastures. We expected the diet composition to follow the widespread pattern with grasses playing a major role. However, since high grazing pressure is restricted to about a third of the total surface of the subalpine pastures in the Park (Krüsi, Schütz, Grämiger & Achermann 1996), and feeding by red deer also occurs in the surrounding forests and alpine grassland, we predicted that the diet would be spatially variable due to higher proportions of tree browse in dung collected in forests. Thirdly, we expected the substantial differences in plant species composition between subalpine pastures studied to show up in the faecal pellets, creating variability at landscape scale.

Material and methods

We sampled fresh faecal pellets of red deer in the Swiss National Park in the canton of Grisons, eastern Switzerland (46°40'N, 10°10'E), during the summer of 2000, a climatically average year. The area is mountainous (ranging within 1,700 - 3,164 m a.s.l.), and consists of 29% subalpine forests, 21% grassland (of which 2% are subalpine and 19% are alpine) and 50% of the area is without vegetation (mainly snow, rocks and scree above the alpine vegetation zone). Forests are mostly dominated by mountain pine, in parts also by Swiss stone pine *Pinus cembra* and larch *Larix decidua*, while Norway spruce *Picea abies* occurs in small proportions and Scots pine *Pinus silvestris* is found locally in the lowest places. Red deer frequent the Park only during summer (June-October) and migrate to lower-lying valleys where they spend the winter on south-facing slopes (Blankenhorn, Buchli & Voser 1978).

For pellet sampling, we chose three subalpine areas in the Park, which are separated by 4, 9 and 12 km. All areas are centred around former cattle pastures which, for the last 80 years, have been grazed only by red deer and chamois (Schütz et al. 2000). The pastures vary considerably in size, elevation and vegetation (Alp La Schera: 16 ha, 2,100 m a.s.l.; Alp Stabelchod: 11 ha, 1,950 m a.s.l.; Plan Mingèr: 1 ha, 1,720 m a.s.l.; considering vegetation see Table 3). Pellets were collected in July, August and September on the three pastures, and in July and September in the forests that surround Alp Stabelchod and Plan Mingèr, but not Alp La Schera. As pellet densities were high on the pastures, we used the grid established for vegetation studies (see below) and chose randomly five grid cells, where we took five pellets (= 1 sample) from each of eight fresh dung heaps. In the surrounding forest, we defined three zones of concentric semicircles in which pellets were collected: 0-100 m from the edge pasture/forest (= forest edge), 100-400 m (= forest interior) and 400-700 m (= upper forest). In the forest, the faecal density was much lower than on the pastures, and the zones were searched randomly until the equivalent of 40 samples was attained in each zone. Thus, we had 40 samples at each pasture/zone and month sampled, which added to a total sample size of 840.

For preparation and analysis, we basically followed de Jong, Gill, van Wieren & Burlton (1995). The frozen pellets were processed in an autoclave after some water had been added. Then, 10 samples were pooled (see Lewis 1994 for the rationale for pooling), leading to a final sample size of 84. The pellets in the pooled samples were crushed and ground in a mortar. From this mixture, five grams were taken and further processed in a lab blender and then rinsed through a sieve of 0.1 mm mesh width. The residue was transferred into 70% alcohol in a petri dish and was allowed to settle for 15 minutes. For analysis, 10 random grab samples consisting of a few drops

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each were taken with a pipette and put on a microscope slide, covered and viewed at 200x magnification. On each slide we identified 10 epidermal fragments on two transects. Using a reticule (0.1 mm grid length) in the microscope ocular we also estimated the fragment area. Eventually, out of the resulting 8,400 fragments (10 fragments x 10 grab samples from 84 pooled samples), 8,337 entered the analysis, and 8,162 were identified to some taxonomic level, thus forming the total sample size.

Results from micro-histological analyses may be biased against species with epidermal cells less well protected by the cuticle, i.e. mostly forbs (Bartolome, Franch, Gutman & Seligman 1995). Such errors may be serious if the results are used to calculate ingested biomass per species, and correction factors have been proposed (Bartolome et al. 1995). As we encountered no more than 2% of totally unrecognisable epidermal fragments (see Results section), and only report fragment numbers and fragment area, we did not subject our results to any *post hoc* correction. However, a relatively high proportion of small fragments, mostly forbs and grasses/sedges (see Table 1), could be identified only at the group but not at species level. This could have been a source of bias that might have affected the various results, if certain species were systematically underrepresented, though this seems unlikely. Forbs were generally well digested and many fragments were simply too small to allow identification. They probably originated from the same (or very closely related) species which also produced the larger fragments that were identifiable to species level. Similarly, not specifically identified fragments in the grass/sedge group were mainly from the upper side of leaves from which stomata are not available to facilitate identification, and were thus likely to be present in similar proportions as fragments from leaf undersides that allowed identification as far as at species level.

For reference, we collected in the study area 40 plant species that were potential deer food items. After being cut in small pieces, the plant material was bleached in 2.5% sodium-hypochloride. Several hours to a few days later, the epidermis could be removed and was mounted on a microscope slide in a preserving layer of glycerine. Of these reference samples, 118 photos were taken and used to identify the epidermal fragments from the pellets.

Considering the vegetation assessment, the vegetation of the pastures was quantified between 1998 and 2001 using relevés on systematic grids with mesh widths of 10x10 m (Plan Mingèr), 20x20 m (Alp Stabelchod) and 40x40 m (Alp La Schera); the different widths were used in response to different pasture sizes. Relevés were made on subplots (1x1 m) in the centre of each grid cell and included determining species composition and abundance (= cover in % of the subplot area) of vascular plants. Sample sizes were 90 relevés on Plan Mingèr, 268 relevés on Alp Stabelchod and 81 relevés on Alp La Schera. From these, the average cover of plant species per pasture was calculated and taken as the abundance value for the entire pasture in question.

Considering the statistical treatment, we measured similarity between samples with the ratio introduced by D. Wishart (van der Maarel, Janssen & Louppen 1978) and implemented in MULVA (Wildi & Orlòci 1996):

$$S_{x,y} = \frac{\sum x_i y_i}{\sum x_i^2 + \sum y_i^2 - \sum x_i y_i} \quad (i = 1, \ldots\ldots, n)$$

where x_i and y_i represent the scores of species i in samples x and y, and n is the number of species.

Results

Overall diet composition and importance of tree browse

Of the 8,337 epidermal fragments selected from the 84 pooled samples, 175 (2%) could not be identified to any taxonomic level and were excluded from the total in all further analyses. Of the remaining 8,162 fragments, 49% (75% in terms of fragment area) were identified as far as at species level, and they belonged to 33 plant species (Table 1). Of the epidermal particles, 51% (25% of fragment area) could only be assigned to one of the following species groups: coniferous tree, dwarf shrub, grass/sedge and dicotyle forb (see Methods section).

The dwarf shrub spring heath *Erica carnea* was the single most common species (in terms of both fragment numbers and fragment area), followed by two grass species (red fescue *Festuca rubra* and blue moor-grass *Sesleria caerulea*). Together, these three species accounted for 33% of all fragments and 51% of the total fragment area, and occurred in all samples. The remaining 30 plant species that were identified as far as to the species level contributed 16% of the fragments and 24% of the fragment area. In terms of taxonomic groups, graminoids (grasses and sedges) were found most often (47% by fragment number and 53% by fragment size), followed by (mainly ericoid) dwarf shrubs (22% by fragment number and 33% by fragment area). As we wanted to know to what extent deer fed in the forest, food plants were categorised according to whether they grow

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Table 1. Plant species identified in the faecal pellet samples of red deer expressed by fragment numbers, fragment area (one unit corresponds to $5x10^{-5}$ mm^2) and frequency of occurrence. * indicates that the species also occurs in subalpine forests. The nomenclature follows Lauber & Wagner (1996).

	No. of fragments	%	Fragment area	%	Frequency of occurrence	%
Forest species						
Picea abies	4	0.0	3196	0.9	4	4.8
Larix decidua	25	0.3	967	0.3	14	16.7
Pinus cembra	25	0.3	4181	1.2	22	26.2
Pinus mugo	13	0.2	2209	0.7	10	11.9
Unidentified coniferous tree	145	1.8	6927	2.1	70	83.3
Juniperus communis	16	0.2	1061	0.3	15	17.9
Daphne mezereum	1	0.0	26	0.0	1	1.2
Arctostaphylos uva-ursi	132	1.6	12749	3.8	56	66.7
Rhododendron hirsutum	5	0.1	274	0.1	4	4.8
Rhododendron ferrugineum	4	0.0	295	0.1	4	4.8
Vaccinium vitis-idaea	201	2.5	10203	3.0	69	82.1
Vaccinium myrtillus	60	0.7	4836	1.4	43	51.2
Erica carnea	1063	13.0	71245	21.1	84	100.0
Unidentified dwarf shrub	309	3.8	9721	2.9	82	97.6
Fragaria vesca	2	0.0	24	0.0	2	2.4
Euphrasia salisburgensis	6	0.1	141	0.0	6	7.1
Campanula rotundifolia	8	0.1	253	0.1	7	8.3
Chrysanthemum leucanthemum	3	0.0	132	0.0	3	3.6
Homogyne alpina	12	0.1	835	0.2	12	14.3
Luzula sylvatica	81	1.0	5482	1.6	46	54.8
Moss species	163	2.0	3959	1.2	57	67.9
Total forest species	2278	27.9	138716	41.1	84	100.0
Grassland species						
Ranunculus montanus	4	0.0	79	0.0	4	4.8
Potentilla crantzii	12	0.1	120	0.0	12	14.3
Alchemilla xanthochlora	2	0.0	23	0.0	2	2.4
Trifolium pratense	17	0.2	797	0.2	14	16.7
Trifolium repens	4	0.0	73	0.0	4	4.8
Plantago media	13	0.2	196	0.1	13	15.5
Senecio abrotanifolius	7	0.1	233	0.1	7	8.3
Leontodon sp.	2	0.0	101	0.0	2	2.4
Hieracium pilosella	58	0.7	868	0.3	31	36.9
Unidentified dicotyle forb	2011	24.6	22991	6.8	84	100.0
Carex caryophyllea	153	1.9	16451	4.9	70	83.3
*Carex sempervirens**	83	1.0	5470	1.6	51	60.7
Festuca rubra	944	11.6	66657	19.8	84	100.0
Briza media	64	0.8	3356	1.0	37	44.0
*Sesleria caerulea**	663	8.1	32380	9.6	84	100.0
Helictotrichon pubescens	155	1.9	5144	1.5	66	78.6
Unidentified grass	1692	20.7	43755	13.0	84	100.0
Total grassland species	5884	72.1	198694	58.9	84	100.0
Total identified plants	8162	100.0	337410	100.0		
Unidentified plants	175		3327		70	83.3

predominantly on grassland or in the forest (see Table 1). Although 72% of all fragments came from grassland species and only 28% from forest plants, the latter attained 41% with respect to fragment area, and remains of forest plant species were present in all samples. Trees, however, were of little importance (2.5% by fragment numbers and 5% by fragment area), although nearly all samples contained small amounts of coniferous tree browse.

Spatial and temporal variation in diet composition

Both the spatial and month-by-month variation in the diet composition was small, as shown by the high similarity values between the three areas (0.927-0.935) and the three months (0.938-0.990; Table 2). The similarity values of within-comparisons were slightly smaller (0.787-0.847) which means that the little variability present in the diet was at the level of the individual sample. Likewise, there were virtually no differences between

Table 2. Comparison of diet composition by fragment numbers (N = 84 samples, see Methods section) between the three study areas and months of sampling.

Area	Alp La Schera	Plan Mingèr	Alp Stabelchod
Alp La Schera	1.0		
Plan Mingèr	0.934	1.0	
Alp Stabelchod	0.935	0.927	1.0
Within-area similarity	0.823 ± 0.072	0.833 ± 0.091	0.824 ± 0.011
Month	July	August	September
July	1.0		
August	0.990	1.0	
September	0.948	0.938	1.0
Within-month similarity	0.847 ± 0.076	0.787 ± 0.098	0.789 ± 0.011

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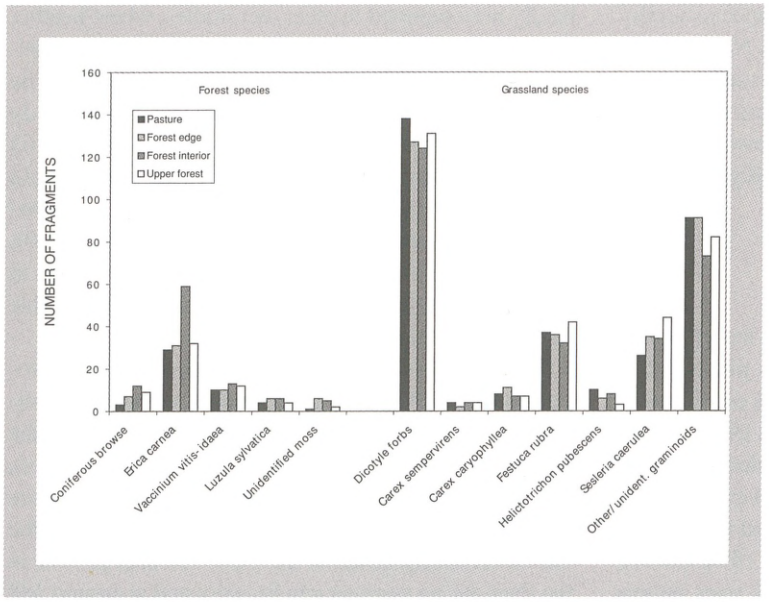


Figure 1. Numbers of fragments of the more important food plant species and species groups in the July samples (N = 16) in the four habitat zones at Alp Stabelchod.

the four habitat zones (grassland, forest edge, forest interior and upper forest) neither at Alp Stabelchod nor at Plan Mingèr (illustrated for Alp Stabelchod in July; Fig. 1). Thus, plant species occurring predominantly on subalpine grassland, and species predominantly from forests were found in similar percentages in the pellets, no matter where the faeces were collected. Minor variation was, however, detected when proportions of grassland and forest plants were related to size of pasture: forest plants made up a higher proportion in the Plan Mingèr area (36% by fragment number and 50% by fragment area) in which the pasture is small (1 ha), as compared to the other two areas (21-25% by fragment number and 31-39% by fragment area) that have pasture sizes of 11 ha and 16 ha, respectively.

Pasture-specific differences in pellet composition were also conspicuously absent when only grassland plants were considered (Table 3). Even though the three pastures differed strongly in size and species composition, in particular with respect to the abundance of graminoids, these differences were not reflected in the faecal pellets that contained many species in relatively similar percentages (e.g. spring sedge *Carex caryophyllea*, evergreen sedge *C. sempervirens*, red fescue, blue moor-grass and downy oat-grass *He-*

Table 3. Abundance of grassland plant species on the pastures of Plan Mingèr, Alp La Schera and Alp Stabelchod (G. Achermann, B. Krüsi, M. Pierik, W. Roetemeijer, M. Schütz and & A. Wirth, unpubl. data), and proportions of the grassland plant species in the faecal pellets collected on the pastures (Diet). Abundance expresses the percentage cover of the more common species; total cover of all species may sum up to more than 100% (max. ca 110%). For this comparison, only grassland plants identified to species are taken into account. - indicates that the species is not represented in the reference collection and thus is not specifically identified in the diet, but may be contained in one of the collective categories, e.g. graminoids, which is not included here (see Table 1).

	Plan Mingèr		Alp La Schera		Alp Stabelchod	
	Abundance	Diet	Abundance	Diet	Abundance	Diet
Forbs						
Ranunculus montanus	5.6	0.0	0.6	0.6	0.2	0.3
Potentilla crantzii	4.8	1.1	0.1	0.3	2.4	0.9
Alchemilla xanthochlora	4.4	0.0	0.3	0.0	1.9	0.3
Trifolium pratense	1.6	1.1	0.6	0.6	1.6	0.9
Trifolium repens	3.9	0.0	2.4	0.3	2.5	0.3
Euphorbia cyparissias	5.6	0.4	0.0	0.0	0.0	0.0
Plantago media	1.0	0.0	0.2	0.3	1.2	1.5
Plantago atrata	0.0	-	0.1	-	3.4	-
Galium pusillum	4.5	-	2.3	-	1.6	-
Achillea millefolium	2.3	-	2.5	-	0.8	-
Senecio abrotanifolius	0.0	0.4	1.4	0.3	1.6	0.3
Cirsium acaule	0.8	-	1.0	-	3.1	-
Hieracium pilosella	4.2	3.0	2.4	3.4	3.3	3.4
Graminoids						
Carex caryophyllea	16.5	8.3	0.8	8.0	3.5	8.0
Carex sempervirens	1.0	7.1	1.7	5.1	14.2	3.4
Festuca rubra	8.2	46.7	1.3	49.3	5.6	34.8
Briza media	8.1	2.6	2.2	6.0	5.1	4.3
Sesleria caerulea	0.4	21.1	0.0	17.1	8.9	29.8
Nardus stricta	0.0	0.0	52.4	0.0	0.0	0.0
Agrostis tenuis	4.2	-	4.1	-	1.3	-
Helictotrichon pubescens	2.4	7.5	0.0	8.0	2.6	11.4
Anthoxanthum odoratum	0.0	-	5.4	-	0.0	-

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lictotrichon pubescens). The only grass species totally absent in the faecal pellets was mat-grass *Nardus stricta*. Most common forbs were taken, but usually at lower proportions than should be expected from their abundance on the pastures, even if one allows for some under representation due to their higher digestibility.

Discussion

Red deer is usually seen as an 'intermediate feeder', somewhat selective towards more nutritious plants while still being able to digest fibrous forage to a considerable degree (Gordon & Illius 1988, Hofmann 1989, Gebert & Verheyden-Tixier 2001). Males can tolerate food of a lower quality than females, and the diet composition may therefore vary between the sexes and age classes (Staines, Crisp & Parish 1982, Osborne 1984, but see also Dzieciolowski 1970). However, as deer pellets are difficult to assign to sex or age class, we did not attempt to classify them; hence, as in most other studies, we report on and discuss an 'overall summer diet'.

Graminoids generally form a major part of the diet, but as an opportunistic feeder (Hofmann 1989), red deer may also eat a wide range of forbs. It regularly browses on leaves, twigs and bark of shrubs and trees, and feeds on seeds and fruit (Goffin & de Crombrugghe 1976, Mitchell, Staines & Welch 1977, Gebert & Verheyden-Tixier 2001). Only few studies have so far reported on the diet composition of red deer in the Alps (e.g. Hegg 1961, Schröder 1977), and some of these studies have not detailed the diet at species level or lack important information on methods applied. Nevertheless, what is known conforms to the general pattern, with grasses dominating in summer (usually 50-60%), followed by forbs (around 20%), dwarf shrubs (≤8%) and tree browse (≤10%). In winter, the proportions of grasses and forbs are generally smaller, while the shares of browse (trees and larger shrubs) and sometimes bark (apart from artificial feeding) are higher.

Summer food composition of red deer in the Swiss National Park was found to be basically similar to the known Alpine pattern, with graminoids accounting for around 50% and tree browse for <10%. Our expectation that the diet composition in the Park would follow a general pattern was thus confirmed. The main exception were dwarf (mainly ericoid) shrubs that had a much higher share (22-33%) than was found elsewhere in the Alps, and also in an earlier study in the Swiss National Park (ca 8%; Hegg 1961). Spring heath, the principal dwarf shrub species eaten, was at the same time the single most abundant species found in our analysis. It has hardly been reported in other diet studies, where heather *Calluna vulgaris* and bilberry *Vaccinium myrtillus* in general are the commonly browsed ericoid shrubs. The latter is common in most Alpine forests, but has only a patchy distribution in the Swiss National Park; on 63 1-m^2 plots in the forest around La Schera, spring heath covered on average 34% of the surface area as compared to the 2% covered by bilberry (Krüsi & Moser 2000). During summer, the digestibility of dwarf shrubs is at its highest, not much below that of forbs and comparable to that of graminoids (Gordon 1989).

Tree browse occurred in most samples but in low proportions (2.5-5%). Assuming that these values constitute an average for both the whole Park area and the entire period of deer being present in the Park (140 days), and further that the mean daily requirements of deer are 2.1 kg dry biomass per animal (Krüsi et al. 1996), the total food consumption of the 2,000 red deer present in the Park during summer can be estimated at around 588 tons dry biomass. The total tree browse would therefore amount to 15-30 tons dry mass, i.e. 30-60 g/100 m^2 of forested area (the total forested area in the Park is 50 km^2). These small quantities, together with data showing that inside the forest an average of 12-17% of the young trees had their terminal shoot browsed (Krüsi & Moser 2000, Kiel 2000), support earlier conclusions that tree regeneration in the Park in general is not hampered by red deer (Krüsi et al. 1996, Kienast et al. 1999, Krüsi & Moser 2000).

We expected to find more temporal and spatial variation in the diet composition than we actually did. The temporal uniformity may reflect that most plant species are simultaneously available during the short alpine summer, and do not show enough differences in the timing of their peak nutritional values to generate a monthly pattern via selective feeding. Spatial variability could have occurred at two scales: at habitat (diets from either forest or pasture) and landscape (differences between the three study areas) scales. The lack of habitat related variability is not surprising and indicates, that deer do not seem to exhibit exclusive feeding preferences for either pastures or forest.

The little variability in the diet found at the landscape scale, i.e. between the three study areas with markedly different grassland vegetation (see Table 3), deserves more discussion. In the course of two days, which is the maximum gut retention time of food in red deer (Illius & Gordon 1992), deer may roam over distances of a few kilometres in Alpine habitats (Georgii 1980, Georgii & Schröder 1983, unpubl. telemetry data from the Swiss National Park and other areas in Switzerland provided by F. Filli, pers. comm., B. Schielly & W. Suter, unpubl.

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data). The study areas, however, are separated by 4, 9 and 12 km and two of them by a high mountain ridge, making it unlikely that deer freely commute between the areas on a daily basis and thus attain a mixed diet. We rather argue that similar faeces compositions are 'convergent', i.e. result from selective feeding.

'Selective' means that resources are used disproportionately to their availability (Manly, McDonald & Thomas 1993). We can test for selectivity only among grassland plants, because we have abundance data for the pasture vegetation (see Table 3), but not for the forest areas. While most forbs were slightly underrepresented in the diet, selection was much stronger for graminoids, resulting in both preference (for sedges *Carex* spp., red fescue in particular, blue moor-grass and downy oat-grass) and partial (e.g. evergreen sedge at Alp Stabelchod) or complete avoidance (mat-grass). In some cases, however, preference must have been less than the high degrees of accumulation (e.g. of red fescue on Alp La Schera from 1.3% on the pasture to 49.3% in the faeces; see Table 3) would suggest, as it is likely that deer grazed patches of graminoid species also outside the studied pastures. This is certainly true for blue moor-grass which occurs in the surrounding forests even where it is absent on the pasture. We also suggest that deer do not select primarily at the level of the individual plant, but at the level of vegetation patches. Previous observations of deer foraging on two other grassland sites in the Park have shown that the animals preferably graze certain patches, but that within the patches, they graze indiscriminately, avoiding only certain larger, unpalatable plants (Märki, Nievergelt, Gigon & Schütz 2000); this resulted in preference for the same graminoid species as found in our study. Thus, even at the local scale, selectivity of food plants does occur at different levels: avoidance both at the level of individual plants and patches, and preference mainly at patch level (see Clutton-Brock, Guinness & Albon 1982).

Selectivity seems to reflect nutritional values and adaptiveness to grazing of the respective species. The strongly preferred red fescue can tolerate heavy grazing and quickly produces fresh shoots with high protein and low roughage content (Märki et al. 2000). This quality makes it also elsewhere a food plant preferred by red deer (Conradt, Clutton-Brock & Guinness 1999) and other wild ungulate species (García-Gonzalez 1984). Mat grass, on the other hand, has a low content of digestible organic matter and rough leaf edges (Schubiger, Bosshard & Dietl 1998) and is known to be avoided in other areas as well (P. Kraus in Bützler 1986).

Acknowledgements - we thank Samuel Isler who assisted in the fieldwork, and Regine Fankhauser and Kathrin Bieri who helped us preparing and identifying plant epidermis particles. Gérald Achermann, Marleen Pierik, Wanne Roetemeijer and Adrian Wirth made vegetation data available, while Flurin Filli, Karin Hindenlang, Josef Senn and two reviewers assisted in improving the manuscript. Thomas Scheurer, Heinrich Haller, Flurin Filli and several Park wardens provided permits, housing and other assistance that made working in the Park a pleasure.

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