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Productivity and usage by red deer (*Cervus elaphus* L.) of two subalpine grasslands in the Swiss National Park

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Summary

1 Produced and by red deer (*Cervus elaphus* L.) consumed phytomass was studied on two subalpine grasslands of different productivity in the Swiss National Park. During three subsequent periods from May to August 1995, a productive ('Il Fuorn'; Trisetetum flavescentis; 3.7 ha; 1790 m a.s.l.) and a less productive grassland ('Stabelchod'; Crepido-Festucetum nigrescentis, Seslerio-Caricetum sempervirentis, Medicagini-Mesobrometum raeticum; 2.6 ha; 1910 m a.s.l.) were compared using a paired-sample design with grazed and ungrazed plots (0.25 m^2). The grassland of Il Fuorn was subdivided in a facies A (without litter) and a facies B (feltlike litter). Both sites were almost exclusively used by hinds and calves. Average densities of red deer were 8–14 individuals per ha on Il Fuorn and 1–4 individuals per ha on Stabelchod per night.
2 During all periods red deer consumed on average 2 g m^{-2} d^{-1} dry matter on facies A of Il Fuorn. Thus, in May and June 85 %, in July 67 % of the produced phytomass were consumed. On facies B the animals consumed in May on average 5.3 g m^{-2} d^{-1} (41% of the produced phytomass), in June 0.7 g m^{-2} d^{-1} (16 %) and in July 3.2 g m^{-2} d^{-1} (54 %) of the plant production. On facies A, the intensive grazing during the growing season resulted in a smaller increase of crude fibre and a smaller decrease of crude protein content compared with facies B.
3 Until mid June, red deer consumed on Stabelchod 0.6 g m^{-2} d^{-1} dry matter (46 % of the produced phytomass). During the two subsequent periods until August, 0.3 g m^{-2} d^{-1} were consumed by red deer. The crude protein and crude fibre content of graminoids of the grazed plots differed after the second period from the ungrazed ones.
4 On both grasslands red deer consumed less than 56 % of the energy available in phytomass. In May and July, red deer met their energy demands on Il Fuorn, in spite of their high density on this site; in June their energy intake on this site was only 60 %. On Stabelchod they met their demands only to 40–74 %, although phytomass was not limited.
5 The results show the differing usage of subalpine grasslands in the Swiss National Park by hinds. The productive grassland Il Fuorn led to a higher concentration of hinds on this site. Since the less productive grassland Stabelchod was only extensively used by red deer, they gathered about 60 % of their energy from the surrounding forests and grasslands.

Keywords: energy budget, fibre content, grazing, net primary production, protein content

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Introduction

When the Swiss National Park (*SNP*) was founded in 1914, only roe deer (*Capreolus capreolus* L.) and chamois (*Rupicapra rupicapra* L.) were present in the *SNP* and its surroundings. Red deer (*Cervus elaphus* L.) was extirpated in the 19th century. Close to the beginning of the 20th century, red deer immigrated from Austria via Prättigau into the Engadine (Luchsinger 1962) and were observed in the *SNP* shortly after its creation. Since that time the population in the *SNP* has increased, and 1476 red deer were counted in 1994 (Schweizerischer Nationalpark 1995). Therefore, the question of the impact of red deer on vegetation is of importance. In the *SNP* and its surroundings, several studies were done on this topic. Hofmann & Nievergelt (1972) investigated the seasonal distribution patterns of ruminants in the valley of Trupchun. Voser (1987) determined the impact of red deer on cultivated meadows in the Lower Engadine and Münstertal. Stüssi (1970) described the succession of different types of grasslands with increasing grazing pressure on Alp la Schera. Hemmi (1991) studied the grazing pressure of ibex (*Capra ibex* L.), red deer and chamois on alpine grasslands in the valley of Trupchun. In cooperation with the study of Hemmi (1991), Zimmermann (1990) investigated the small-scale pattern of vegetation use. Bonfils (1989) studied the effects of ungulate trampling on vegetation cover and erosion of alpine grasslands. Results from long-term studies on permanent plots, established up-to 80 years ago, indicate that the present impact of red deer and chamois is too low, rather than too high, to preserve the percentage of grassland in the *SNP* (Krüsi *et al.* 1995).

In spring, during periods of unfavourable weather in summer, and in late autumn, red deer graze preferably on subalpine pastures. Within the *SNP* there are only few, small grasslands in the subalpine zone, and they are usually heavily grazed (Voser 1987). In the region of Il Fuorn these grasslands are Alp la Schera, Il Fuorn, Stabelchod, and three others.

In the present study, the productivity of the subalpine grasslands of Il Fuorn and Stabelchod and the grazing intensity of red deer are compared. For that purpose, phytomass production and its consumption by red deer, as well as the seasonal variation of crude protein and crude fibre content were measured during one growing season. With these data the required and the consumed energy of the red deer as well as energy available in the grassland vegetation were calculated to judge the significance of the two subalpine grasslands as food resources for red deer.

Methods and study sites

STUDY SITES

The study was carried out in the region of the Ofenpass in the eastern Central Alps. It is characterized by a continental climate with low precipitation (974 mm per year). As study sites, the grassland Il Fuorn (Coord. 811 860/171 750; 3.7 ha, 1790 m a.s.l) and the grassland of Stabelchod (Coord. 814 500/171 400; 2.6 ha, 1910 m a.s.l.) were chosen. Both subalpine grasslands are bounded mainly by the pass and by Erico-Pinetum mugo (nomenclature of plant communities follows Zoller 1995).

Il Fuorn was in agricultural use until 1970. Since then the grasslands have been cut only a few times. Well weathering bed rock (Verrucano), location at the base of a slope, good water supply, as well as nutrients of the former agriculture favour plant growth. Campell & Trepp (1968) described the grasslands of Il Fuorn as varieties of a Trisetetum flavescentis.

Stabelchod is a dryer grassland which was used as a pasture until the foundation of the *SNP;* former irrigation ditches are still visible. The grassland lies on an alluvial fan of dolomite and shows a mosaic of three plant communities that indicate less nutrient-rich conditions (Crepido-Festucetum nigrescentis, Seslerio-Caricetum sempervirentis, Medicagini-Mesobrometum raeticum).

RED DEER

The red deer population of the *SNP* uses different summer and winter home ranges (Voser 1987). Between the end of April and the beginning of June they migrate periodically on traditional routes from the winter habitats in the Engadine and Münstertal to the summer habitats within the *SNP.* The migration from summer to winter habitats usually begins in October after the rut, but can start in August or late in November, depending on weather conditions and food resources.

Fig. 1 shows the densities of red deer during 1995 on both study sites. About one week after the snow had melted, the first red deer were sighted on the grassland Il Fuorn. During the whole period investigated, only hinds and calves grazed on both study sites, whereas chamois and roe deer were rarely observed. Stags used the study sites mainly at the end of summer and during the rut. The average densities of red deer were always higher on Il Fuorn than on Stabelchod.

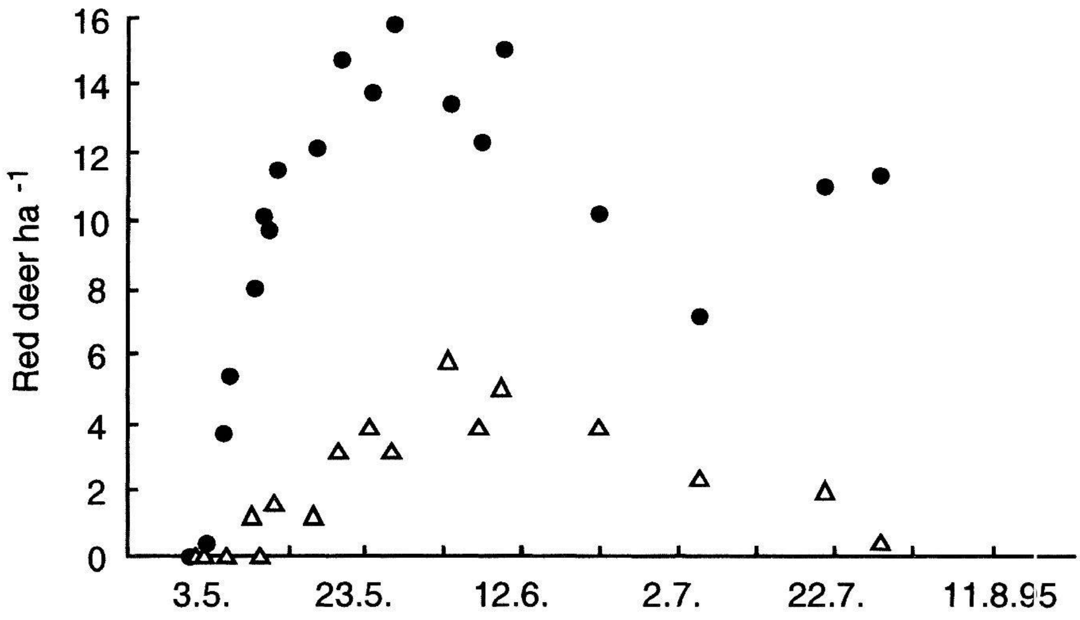

Fig. 1. *Densities of red deer on the study sites Il Fuorn (●) and Stabelchod (△) (Parkdirektion 1995).*

CONSUMED PHYTOMASS

The phytomass consumed by red deer was calculated by means of the difference method (Klapp 1971; Cox & Waithaka 1989). A paired-sample design was used on both study sites, where a grazed and an ungrazed plot (each 50 cm x 50 cm; distance 2.5 – 4 m) formed pairs for observation. Grazed control and ungrazed experimental plots were located randomly. The experimental plots were protected from grazing by wired off exclosures (70 cm x 70 cm x 60 cm; mesh size 20 mm) with a strip of 10 cm as a buffer zone around the plots.

Experimental design

At the beginning of the study, the grassland of Il Fuorn was subdivided in a facies A (without litter; N = 14) and a facies B (with feltlike litter; N = 6). The amount of litter of a given plot depends on the grazing pressure of the previous year which in turn is a product of species composition (Achermann 1995).

The difference method overestimates the consumed phytomass, if it is applied for long grazing periods, because of the undisturbed growth on the ungrazed plots (Linehan *et al.* 1952; Klapp 1971). Hence the consumed phytomass was determined after three to four weeks. From May to August 1995, both grasslands Il Fuorn and Stabelchod (N = 15) were studied during three subsequent periods. Due to a long period of unfavourable weather in June, the first period was prolonged on Il Fuorn (36 days, only facies A) and on Stabelchod (43 days) in comparison to the second and third period (each about 24 days).

After each period the paired samples were set up on previously grazed areas.

Clipping

At the end of each period, the grazed control and ungrazed experimental plots were clipped at 1.5 cm above ground. This corresponds to the lowest cropping height of red deer on facies A.

The dry weight (*DW*) of the plant material was determined separately for graminoids (Cyperaceae, Juncaceae and Poaceae), forbs, and dead plant material. Afterwards, the nutritional value of the dried plant material was determined.

NUTRITIONAL VALUE

The crude protein (RAP-ME11403O.710) and crude fibre content (RAP-ME 10901O.710) of three samples of both graminoids and forbs were analysed at the Swiss Federal Research Station for Animal Production (*RAP*) in Posieux for the control and the experimental plots of each study site and period. For technical reasons, only three samples could be analysed for each category; hence no statistical analyses were performed.

CALCULATIONS

(1) New growth (g DW m^{-2}) = (Sampled phytomass at the end of each period; for both experimental and control plots) – (Average phytomass of the previous period on the control plot).

(2) Rate of consumption (g DW m^{-2} d^{-1}) = [(Average phytomass on experimental plot) – (Average phytomass on control plot)] (Number of days)$^{-1}$.

(3) Rate of production (g DW m^{-2} d^{-1}) = [(Average phytomass on experimental plot) – (Average phytomass on previous control plot)] (Number of days)$^{-1}$.

(4) Density of red deer (N ha^{-1}): The number of red deer per area was calculated separately for hinds and calves based on data of Parkdirektion (1995).

(5) Energy requirement of red deer (MJ ha^{-1}): The requirement depending on body weight (BW in kg) was calculated as follows: Requirement $= x\,BW^{0.75}$ (Bubenik 1984). For hinds, x was estimated as 1.26 MJ per kg BW because of lactation (Bubenik 1984), which amounts to 33.6 MJ per hind per day for a body weight of 80 kg (Blankenhorn *et al.* 1979). For calves, x was assumed as 0.67 MJ per kg BW. Because the BW of calves increased during summer, the energy requirement per calf increased from 7.5 MJ d^{-1} during the first period to 9.6 MJ d^{-1} during the second period and to 10.7 MJ d^{-1} during the third period.

(6) Digestible energy content (MJ kg^{-1}): The digestibility of the organic matter in per cent was calculated for both graminoids

and forbs using crude fibre content. The digestible crude protein was calculated on the basis of crude protein content. The digestible energy (MJ kg^{-1}) was calculated using digestible crude protein and digestible organic matter (Forschungsanstalt für viehwirtschaftliche Produktion, Posieux, Schweiz, 1994: pp. 311–312).

(7) Available and consumed energy (MJ d^{-1}): The available and consumed energy per day were calculated for both graminoids and forbs by multiplication of the rate of production and consumption by the digestible energy content. Numbers in Table 1 are the sum of energy of graminoids and forbs. On the grassland Il Fuorn, the amount of facies A and B in relation to the total area were estimated $^2/_5$ and $^3/_5$, respectively.

Results

FOOD SUPPLY AND CONSUMPTION

Il Fuorn (A)

The dry weight *(DW)* of the aboveground phytomass increased from the first to the third period on the steadily grazed plots from 12 to 47 g m^{-2}. The highest new growth occurred during the third period with 24 g m^{-2}, and was mainly caused by the new growth of graminoids (Fig. 2).

At the end of all periods, the *DW* of the phytomass was significantly higher on the ungrazed experimental plots than on the grazed control plots ($P < 0.002$, Wilcoxon test). The rate of consumption increased by 0.3 g m^{-2} d^{-1} from the first to the second period and then remained stable at 2.2 g m^{-2} d^{-1}. During the first and second periods 85 % of the new growth was consumed, during the third period 67 %.

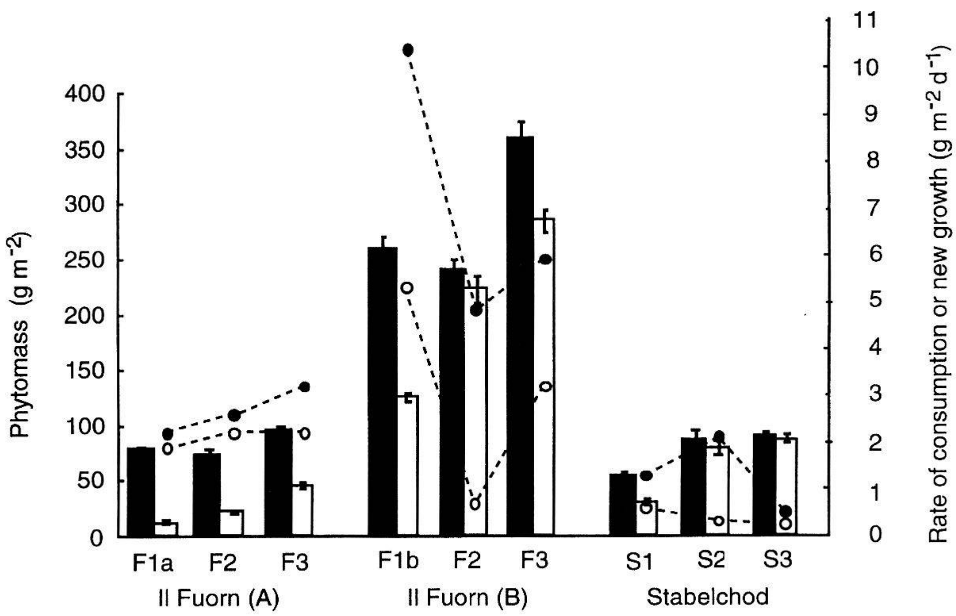

Fig. 2. Phytomass (g m⁻²) of ungrazed experimental (■) and grazed control (□) plots (mean ± 1 SE) of Il Fuorn (A) (facies A, without litter), Il Fuorn (B) (facies B, with feltlike litter) and Stabelchod; additionally, the calculated rate of production (●) and consumption (○) (g m⁻² d⁻¹) are given. F1a, 5.5.–10.6. (36 d); F1b, 15.5.–10.6. (25 d); F2, 10.6.–4.7. (24 d); F3, 5.7.–28.7. (23 d); S1, 10.5.–22.6. (43 d); S2, 22.6.–19.7. (27 d); S3, 20.7.–11.8. (22 d).

Il Fuorn (B)
During the three periods, the phytomass *(DW)* increased on the steadily grazed plots from 127 g m^{-2} to 286 g m^{-2} (Fig. 2). The phytomass after the first and third period was significantly higher on the ungrazed plots than on the grazed ones *($P < 0.05$*, Wilcoxon test). During the first period, the rates of production and consumption (10 g m^{-2} d^{-1} and 5 g m^{-2} d^{-1}) were higher on facies B than on facies A. During the first period 41%, during the second 16%, and during the third 54% of the new growth was consumed.

Stabelchod
From the first to the third period, the phytomass *(DW)* on the steadily grazed plots increased from 30 g m^{-2} to 85 g m^{-2} (Fig. 2). During the second period, the rate of production reached its peak with 2 g m^{-2} d^{-1}. However, during all periods the rates of production were always lower on Stabelchod than on Il Fuorn.

During the first period, the rate of consumption on Stabelchod (0.6 g d^{-1} m^{-2}) was about three times lower than on facies A of Il Fuorn. Only after the first period was the *DW* of the phytomass significantly higher on the experimental plots than on the control plots ($P < 0.002$, Wilcoxon test). During the second period, the rate of consumption was 0.3 g m^{-2} d^{-1} and decreased to 0.2 g m^{-2} d^{-1} during the third period.

During the first period 46% of the new growth was consumed, during the second 14%, and during the third 33%.

CRUDE PROTEIN AND CRUDE FIBRE CONTENT

Il Fuorn
Crude fibre content of graminoids on ungrazed plots increased from the first to the second period from 190 g kg^{-1} (facies A) and 250 g kg^{-1} (facies B) for both facies by about 60 g kg^{-1} (Fig. 3a). The heavily grazed control plots of facies A showed the same high value at the end of the third period as the ones of facies B at the end of the first period.

Crude protein content of graminoids decreased from the first to the third period by about 30 g kg^{-1} on the grazed control plots of facies A and amounted to 200 g kg^{-1} by the third period. On facies B, the decrease from 250 g kg^{-1} to 150 g kg^{-1} in crude protein content of graminoids was three times higher than on facies A. At the beginning of the growing season, crude fibre and crude protein content were similar on both facies A and B. However, in the course of the growing season, steady grazing on facies A caused for both graminoids and forbs to a smaller increase in crude fibre and a smaller decrease in crude protein content than on facies B.

Facies A differed from facies B also with respect to the nutritional value of forbs (Fig. 3b). Crude protein content of forbs decreased from the first to the second period on the control plots of facies A from 258 g kg^{-1} to 238 g kg^{-1} and then increased to 246 g kg^{1}. Crude protein content of forbs on facies B decreased from the second to the third period from 215 g kg^{-1} to 160 g kg^{-1}; no data are available for the first period. Crude fibre content of forbs on facies B was 200 g kg^{-1} during at the third period, whereas on facies A it amounted to only 155 g kg^{-1}.

Stabelchod
Only at the end of the second period did the crude fibre and crude protein content of graminoids on the experimental plots differ appreciably from the grazed control plots. During all periods, the crude fibre content of forbs from the grazed plots was smaller by 10 g kg^{-1} than that of the ungrazed experimental plots (Fig. 3b).

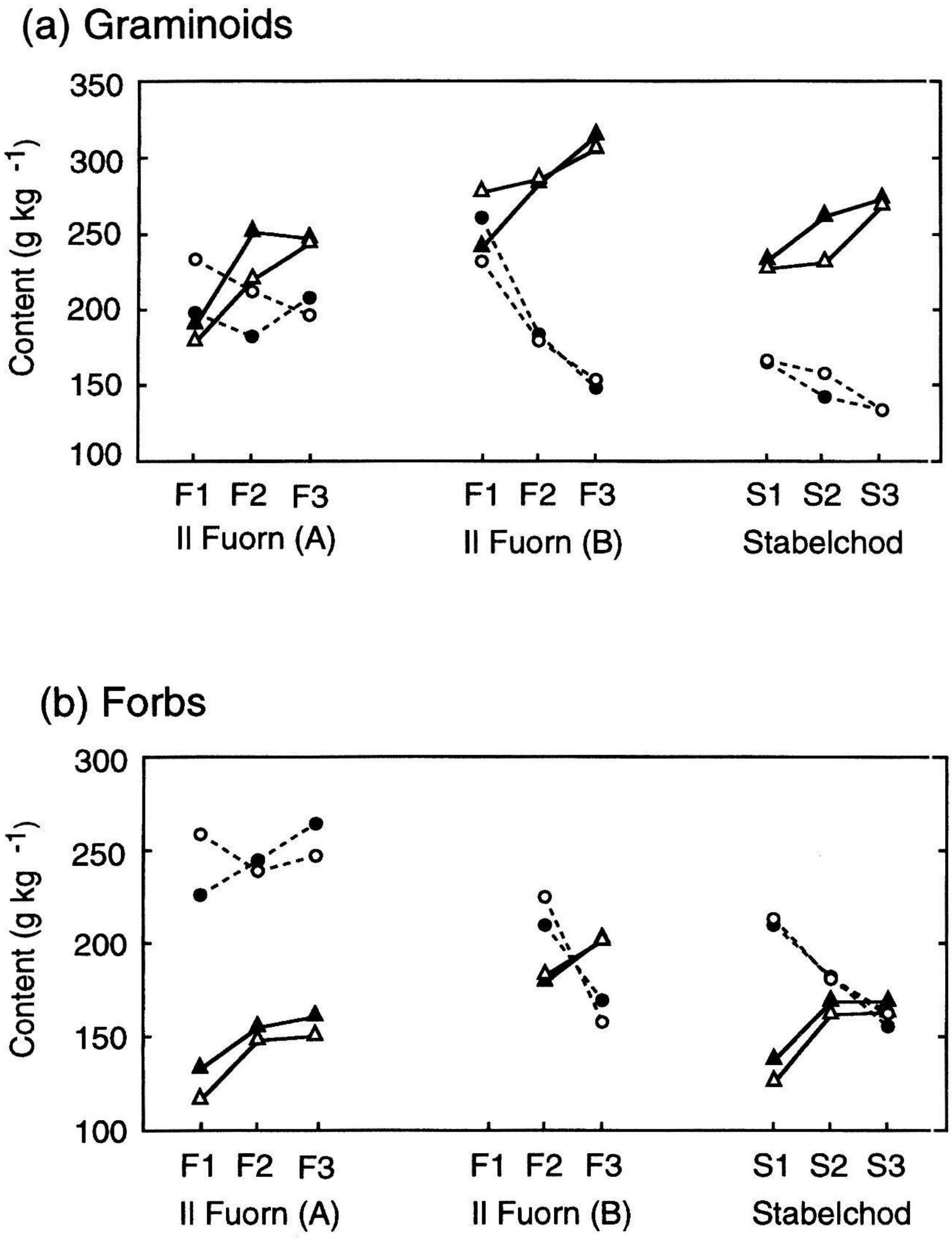

Fig. 3. Changes in crude fibre (▲△) and crude protein (●○) content of (a) graminoids and (b) forbs (mean of three samples) on Il Fuorn (A), Il Fuorn (B) and Stabelchod. Filled symbols, ungrazed experimental plots; open symbols, grazed control plots.

ENERGY BUDGET OF RED DEER

During the first and third period, red deer nearly met their daily energy requirements with their energy intake on Il Fuorn (Table 1). Thus, they consumed about 56% of the energy available in vegetation. During the second period red deer met only 59% of their daily energy requirements on this grassland. During the first and third periods phytomass energy was not limiting, however, the red deer consumed only 34% of the available energy.

During the first observation period on Stabelchod, red deer met only 72% of their energy requirements from this grassland, although with 54% a similar amount of the available energy was consumed as on Il Fuorn (Table 1). To meet their requirements, 76% of the available energy should have been consumed. During the second and most productive period on Stabelchod there was about the same density of red deer on this grassland as during the first period. However, they consumed only 14% of the available energy and thus met their energy requirements only to 40%. During the third period they met 75% of their daily requirements by the consuming 32% of the available energy, but the average density of red deer was about three times smaller than during the first and second periods.

***Table 1.** Energy budget of red deer on two subalpine grasslands (Il Fuorn, Stabelchod). Comparison of energy requirement of red deer (R), energy available in phytomass (A) and energy consumed by red deer (C). Three energy ratios enable comparison of the three periods of observation and the two study sites*

Site	Red deer ha^{-1}		Energy (MJ ha^{-1} d^{-1})			Energy ratios		
Period	Hinds	Calves	R	A	C	$C R^{-1}$	$R A^{-1}$	$C A^{-1}$
Il Fuorn								
F1 (5.5.-10.6.)	11.9	1.3	410	799	445	1.09	0.51	0.56
F2 (11.6.-4.7.)	7.4	0.8	253	431	148	0.59	0.59	0.34
F3 (5.7.-28.7.)	8.8	1.0	311	515	294	0.95	0.60	0.57
Stabelchod								
S1 (10.5.-22.6.)	2.8	1.1	99	131	71	0.72	0.76	0.54
S2 (23.6.-19.7.)	2.3	0.9	85	240	34	0.40	0.35	0.14
S3 (20.7.-11.8.)	0.8	0.3	30	69	22	0.74	0.44	0.32

On Il Fuorn, red deer consumed a larger proportion of the energy available in phytomass in comparison to Stabelchod (34–57%). Only during the first period was a similar amount (54%) consumed on Stabelchod. However, the average density of red deer was about four times higher and available energy about nine times higher on Il Fuorn than on Stabelchod. During the second and third periods on Il Fuorn, the three to nine times higher densitiy of red deer consumed about twice the amount of the energy available compared to Stabelchod.

Interestingly, during the second period, red deer met only 59% and 40% of their energy requirements on the two grasslands, i.e. about 55% of the consumed energy during the corresponding first and third periods. During all periods, consumption of energy required was lower by 20–30% on Stabelchod compared to Il Fuorn.

Discussion

Phytomass and new growth were smaller on Stabelchod than on Il Fuorn. This is probably caused by the difference of 120 m in elevation, and by the well weathering bed rock (Verrucano), and the better water supply on Il Fuorn. Nutrients of the former agriculture may also play a role on Il Fuorn, whereas the geological substrate of Stabelchod is clearly less nutrient-rich (alluvial fan of dolomite).

In May, soon after the snow had melted, the first hinds were observed on Il Fuorn and Stabelchod. Atzler (1984) suggested that seasonal migrations of red deer adapt to spatial and temporal changes in quality of food. In May, crude fibre content increases at lower elevations, whereas at higher altitudes, fibre content of graminoids and forbs remains low because of delayed growth (Georgii 1980). In May or June hinds give birth to their calves. The observed concentration of hinds on Il Fuorn may be caused by the fact that hinds, compared to stags, prefer more nutrient-rich grasslands for grazing (Charles *et al.* 1977; Osborne 1984) in order to meet their higher energy requirements due to pregnancy and lactation (Staines *et al.* 1982). In addition, the subalpine grasslands of the *SNP* are surrounded by large forests, which provide shelter for hinds and calves.

Atzler (1984) stressed the importance of protein and fibre content for the quality of food. Bonengel (1969) showed with feeding trials that red deer are able to select fodder with a high protein content. Moss *et al.* (1981) also observed highest grazing pressure of red deer on the most nutrient-rich places. During the growing season, crude protein and crude fibre content developed inversely in undisturbed vegetation: Protein content of plants decreased whereas fibre content increased, both on facies B of Il Fuorn and on Stabelchod. However, steady grazing during the growing season on facies A of Il Fuorn led both graminoids and forbs to smaller increases of fibre content and smaller decreases of protein content than on facies B, although both facies showed a similar fibre and protein content at the beginning of the season. Therefore, the grassland of Il Fuorn and especially facies A are of a high quality and important for red deer. Clutton-Brock & Albon (1989) observed that red deer prefer lawn-like turfs similar to facies A of Il Fuorn.

A three to nine times higher density of red deer was observed on Il Fuorn as compared to Stabelchod. Despite this higher density, red deer could satiate their energy requirements by consuming 51–60 % of the energy available on Il Fuorn, which they actually did during the first and third observation periods. Red deer never met their daily energy requirements exclusively on Stabelchod, although it would have been possible with the observed average density of 1–4 red deer per hectare. The differing composition of species on Stabelchod and Il Fuorn (Achermann 1995) may have led to a more pronounced food selection on Stabelchod, and consequently to a smaller intake. By analysing long-term studies, Krüsi *et al.* (1995) concluded that the impact of red deer and chamois is rather too low to preserve the percentage of subalpine grasslands in the *SNP*. If consequently the open areas become scarce in the subalpine belt, a local decrease in botanical diversity will result.

If red deer are undisturbed during the day, they keep a regular pattern of grazing periods. In regions with frequent disturbance, however, the grazing periods are prolonged during the night, which can lead to an increase in browsing or removal of the bark in the resting quarters during the day (Bützler 1991). On Il Fuorn and Stabelchod, red deer grazed only during the night because of disturbances by tourists. Since red deer met their energy requirements only during the first and third periods on Il Fuorn, they must have had additional food during all other periods (including the ones of Stabelchod) from the surrounding forests or in nearby scrub *(Pinus mugo)* or alpine grasslands. Bützler (1991) stressed in this context the physiological significance of additional food from trees or shrubs for digestion of red deer. Based on faeces analysis in the *SNP*, Hegg (1961) showed that summer food of red deer consists to 35 % of graminoids, to 40 % of forbs and to 25 % of evergreen plants. Unfortunately, this study provides no information about the places where faeces were collected. To answer the question of how much food is grazed in alpine grasslands or browsed in the surrounding forests, new analyses of faeces are necessary.

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References

Achermann, G. (1995) *Kleinräumige Nutzung von zwei subalpinen Rasen durch Rothirsche* (Cervus elaphus *L.) im Schweizerischen Nationalpark.* Diploma thesis, Geobotanical Institute ETH, Zürich.

Atzler, R. (1984) Nahrungsangebot und Wanderverhalten von Rothirschen in den Ammergauer Bergen. *Zeitschrift für Jagdwissenschaft,* **30**, 73–81.

Blankenhorn, H. J., Buchli, C., Voser, P. & Berger, C. (1979) *Bericht zum Hirschproblem im Engadin und im Münstertal.* Proget d'ecologia. Anzeiger-Druckerei, St. Gallen.

Bonengel, H. (1969) *Fütterungsversuche bei heranwachsendem Rotwild* (Cervus elaphus hippelaphus *Erxleben, 1771).* PhD thesis, Institut für Tierphysiologie, University of München.

Bonfils, P. (1989) *Einfluss der Trittbelastung von Huftieren auf die Erosionsgefährdung von Böden im Schweizerischen Nationalpark.* Diploma thesis, Institut für Wald- und Holzforschung ETH, Zürich.

Bubenik, A. B. (1984) *Ernährung, Verhalten und Umwelt des Schalenwildes.* BLV, München.

Bützler, W. (1991) *Rotwild: Biologie, Verhalten, Umwelt, Hege.* BLV, München.

Campell, E. & Trepp, W. (1968) Vegetationskarte des Schweizerischen Nationalparkes. Beschreibung der Pflanzengesellschaften von W. Trepp. *Ergebnisse der wissenschaftlichen Untersuchungen im Schweizerischen Nationalpark,* **58**, 1–42.

Charles, W. N., McCowan, D. & East, K. (1977) Selection of upland swards by red deer *(Cervus elaphus* L.) on Rhum. *Journal of Applied Ecology,* **14**, 55–64.

Clutton-Brock, T. H. & Albon, S. D. (1989) *Red deer in the Highlands.* BSP Professional Books, Oxford.

Cox, G. W. & Waithaka, J. M. (1989) Estimating aboveground net production and grazing harvest by wildlife on tropical grassland range. *Oikos,* **54**, 60–66.

Forschungsanstalt für Viehwirtschaftliche Produktion, Posieux, Schweiz (eds.) (1994) *Fütterungsempfehlungen und Nährwerttabellen für Wiederkäuer.* Landwirtschaftliche Lehrmittelzentrale, Zollikofen.

Georgii, B. (1980) Home range patterns of female red deer *(Cervus elaphus* L.) in the Alps. *Oecologia,* **47**, 278–285.

Hegg, O. (1961) Analysen von Grosswildkot aus dem schweizerischen Nationalpark zur Ermittlung der Nahrungszusammensetzung. *Revue Suisse de Zoologie,* **68**, 156–165.

Hemmi, M. (1991) *Äsverhalten und Äsungsdruck von Steinbock, Rothirsch und Gemse auf einer alpinen Weide im Schweizerischen Nationalpark.* Diploma thesis, Zoological Institute, University of Zürich.

Hofmann, A. & Nievergelt, B. (1972) Das jahreszeitliche Verteilungsmuster und der Äsungsdruck von Alpensteinbock, Gemse, Rothirsch und Reh in einem begrenzten Gebiet im Oberengadin. *Zeitschrift für Jagdwissenschaft,* **18**, 185–212.

Klapp, E. (1971) *Wiesen und Weiden. Eine Grünlandlehre.* Parey, Berlin.

Krüsi, B.O., Schütz, M., Wildi, O. & Grämiger, H. (1995) Huftiere, Vegetationsdynamik und botanische Vielfalt im Nationalpark. Ergebnisse von Langzeitbeobachtungen. *Cratschla,* **3**, 14–25.

Linehan, P. A., Lowe, J. & Stewart, R. H. (1952) The output of pasture and its measurement (III). *Journal of the British Grassland Society,* **7**, 73–24.

Luchsinger, M. (1962) *Das Rotwild in der Schweiz. Verbreitung, Entwicklung und Wanderwege in den Schweizer Alpen.* Report, Zoological Institute, University of Zürich.

Moss, R., Welch, D. & Rothery, P. (1981) Effects of grazing by mountain hares and red deer on the production and chemical composition of heather. *Journal of Applied Ecology,* **18**, 487–496.

Osborne, B. C. (1984) Habitat use by red deer and hill sheep in the West Highlands. *Journal of Applied Ecology,* **21**, 497–506.

Parkdirektion (1995) *Ergebnisse der Huftierzählungen von Il Fuorn und Stabelchod.* Internal report, Zernez.

Schweizerischer Nationalpark (1995) *Geschäftsbericht 1994.* Eidgenössische Nationalparkkommission und Stiftung Nationalparkhaus, Zernez.

Staines, B.W., Crisp, J.M. & Parish, T. (1982) Differences in the quality of food eaten by red deer *(Cervus elaphus* L.) stags and hinds in winter. *Journal of Applied Ecology,* **19**, 65–77.

Stüssi, B. (1970) Naturbedingte Entwicklung subalpiner Weiderasen auf Alp La Schera im Schweizerischen Nationalpark während der Reservatsperiode 1939–1965. *Ergebnisse der wissenschaftlichen Untersuchungen im Schweizerischen Nationalpark,* **61**, 1–385.

Voser, P. (1987) *Einflüsse hoher Rothirschbestände auf die Vegetation im Unterengadin und im Münstertal, Kanton Graubünden.* PhD thesis, University of Zürich.

Zimmermann, B. (1990) *Wechselwirkungen zwischen alpinen Rasen und freilebenden Huftieren im Schweizerischen Nationalpark: Produktion, Konsumation, Selektivität.* Diploma thesis, Institute for Systematic Botany, University of Zürich.

Zoller, H. (1995) *Vegetationskarte des Schweizerischen Nationalparks. Erläuterungen.* Nationalpark-Forschung in der Schweiz, **85**, 1–108.

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