An Individual-based Model of the Summer Energy Budget of Red Deer (*Cervus elaphus* L.) in the Swiss National Park

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Abstract

While the estimation of the carrying capacity of red deer (*Cervus elaphus* L.) in the Swiss National Park until now was based on seasonal mean phytomass productivity, we present a new approach which accounts for seasonal changes in the vegetation and the physiology of red deer during a growing season.

Our approach roots in an individual-based simulation model of the foraging behavior during the growing season in the Swiss Alps (May - October). The model assumes that red deer physiology and behavior lead to a maximization of energy intake during summer to compensate for winter weight losses. Maximal daily energy intake is constraint by the time needed for grazing plus forage digestion. We used a Michaelis-Menten functional response to parameterize the grazing. Digestion is a function of forage quality and is formulated as an exponential decay of rumen fill. A vegetation model calculates phytomass quantity as logistic growth. Phytomass quality (crude protein and fiber content) decreases linearly with the increasing phytomass quantity. Vegetation consists of four vegetation types: subalpine grassland, subalpine meadows, alpine meadows, and subalpine forest.

Our modeling of the interaction between red deer and vegetation helped us to identify critical temporary conditions during the growing season: For instance the demand supply ratio was most critical in spring. The non-linearity of the functional response was found to be crucial for any reliable estimation of the carrying capacity.

Introduction

Overgrazing stays for an excess of herbivory which leads to the degradation of an ecosystem (Coughenour & Singer 1996). From a management perspective overgrazing has to be defined on the basis of human valuation (Coughenour & Singer 1996). Overgrazing is an undesirable impact from herbivores on their resources and ecosystem. In the case of wilderness reserves such as the Swiss National Park (SNP) or the Yellowstone Park (Coughenour & Singer 1996) the problem of overgrazing relates to the estimation of the size of a natural herbivore population.

The issue then is how to define a natural deer population in space, how to estimate its size, and how to discern a natural from an anthropogenic induced population regulation. In the case of the SNP anthropogenic alteration of population regulation is most pronounced for three factors: the absence of large predators, food availability in the winter ranges outside the park, and thirdly the fact that deers are also hunted outside the park.

There is an on-going debate whether these anthropogenic interferences lead to an undesirable or unnaturally high deer population density within the park. Blankenhorn et al. (1979) have postulated that a population number of about 2’440 individuals at the end of the 1970s exceeded a maximal desirable size for the SNP. They have argued that this lead to higher winter mortality, competition pressure on chamois, overgrazing on subalpine meadows and reduced rejuvenation of the forests in the park.

Recently the focus of this scientific debate has been on the interaction of the vegetation and the herbivores within the park during the growing season. Two main direction of research clarified aspects of the interaction of deer and vegetation in the park:

A first approach has surveyed the impact of herbivore disturbances on grassland biodiversity. Theoretical background is the “intermediate disturbance hypothesis” (Connell 1978). Results from succession research on subalpine meadows in the SNP have revealed a positive correlation between species richness of phanerogams and the number of red deer (Schütz et al. 2000). A reduction of forest regrowth by red deer has been doubted (Schütz et al. 2000). However, this approach provides little support for a quantitative deer management.

A second approach (Holzgang 1997) has estimated the herbivore carrying capacity of the SNP according to the classical logistic growth equation. Carrying capacity is thus defined as the maximum population size where saturation is reached (Nicholson 1974). These approaches have assumed that deer populations are limited by food availability (Hairston et al. 1960) and consequently estimate carrying capacity by calculating total phytomass productivity, by measuring nutritive value of the forage as energy supply and by estimating the per capita mean daily energy demand by red deer (Holzgang 1997, Paton et al. 1999).

However, more recent results indicate that populations of large herbivores are mainly regulated by stochastic fluctuations in the environment both during summer and winter

(Saether 1997) and by the winter mortality of calves (Clutton-Brock et al. 1985, Gaillard et al. 1998). This indicates that extreme conditions rather than mean values are relevant for an understanding of limiting environmental conditions. Since an estimate merely based on seasonal mean data ignores spatial and temporal heterogeneity of forage availability and energy requirements, neither bottlenecks of food scarcity nor extremes of grazing pressures can be identified.

In this study a dynamic model of the availability of forage quality and quantity and of energy requirements throughout the growing season was used to study the grazing dynamics. The model is an individual-based computer simulation model. It consists of four coupled submodels: a plant growth model, plus three submodels for deer foraging, movement, and physiology respectively. The model was based on assumptions and data taken from optimal foraging theory (Stephens & Krebs 1986) and from ruminant physiology.

Instead of most foraging models of large herbivores that have been used to test hypothesis of optimal foraging (Bergman et al. 2001, Fryxell 1991, Wilmshurst et al. 1999), we used the model to study herbivore vegetation interactions at the population scale. Combination of behavior and population biology is an emerging and promising field in current animal ecology (Bradbury et al. 2001, Lima & Zollner 1996). Moreover, since in most existing foraging models digestion constraint is not modeled explicitly (Bergman et al. 2001, Moen et al. 1997), our objective was to present a new foraging model for red deer (Fryxell 1991) inasmuch as it explicitly models the digestive constraint. Based on our model we will discuss earlier estimates of carrying capacity, and demonstrate that the precise mechanisms of interaction between deer and vegetation determine the deer's energy budget only at critical points in time and only under rare, special conditions.

Methods

The Study Site

Data on the vegetation, the structure of the deer population and the behavioral activity patterns have all been collected in the Swiss National Park (SNP). The SNP is located in the Engadine Valley within the European Alps in the south-eastern part of Switzerland. Currently the park occupies a high, mountainous region of 170 km^2, which ranges from 1'500 to 3'170 m.a.s.l. Annual rainfall amounts to about 1'140 mm (Committee for scientific research in the National Park 1966). The ground consists basically of calcareous sediments. The vegetation (forests, subalpine and alpine grasslands) covers around 50% of the total area (Zoller 1995).

Since its establishment as a nature reserve in 1914 the SNP is strongly protected from any human influences. Since 1914 no agricultural or silvicultural practices have been allowed and as long as an animal stays within the park, it is protected from hunters. Visitors are not allowed to leave the trails.

However, before the park was founded the subalpine grasslands were heavily grazed by cattle and the few remaining forests were depleted by intensive harvesting (Parolini 1995). Thereafter the population of red deer (*C. elaphus*) grew rapidly from only a few individuals at the beginning of the last century to a maximum of about 2'400 individuals around 1980 (Blankenhorn et al. 1979). Since then the population remained more or less constant as a result of hunting in the surrounding areas of the park. Red deer use the Park from May to October as their summer range. In winter most deer leave the park and stay in the adjacent lower valleys.

The actual study area has been restricted to an area of 1'500 ha around Il Fourn (Coordinates 81'000.0 – 816'000.0; 170'500.0 – 173'000.0) within the inner part of the SNP. The boundaries of the study area were defined by the home ranges of the individual animals living in this area (Altherr 1999). The area contains 1'030 ha of forest, 95 ha of subalpine meadows, 10 ha of subalpine grassland, and 140 ha of alpine meadows.

Model Validation

The model was not validated in a strict sense. Instead we compared the results of a standard simulation run with data and information from the literature. The standard simulation run lasted 150 days (15th May to 12th October - it was assumed that within this period red deer stay always within the SNP, i.e. within their summer range), took place on a subalpine grassland, and started with a red deer population density which corresponds to 1 animal per ha. Based on the assumption that forage availability should be optimal under these conditions, we compared simulated daily dry matter intake, activity patterns, i.e. mean fraction of a day an animal is active, and seasonal weight changes qualitatively with data of red deer as found in the literature (Blankenhorn et al. 1979, Bützler 1991, Clutton-Brock et al. 1982, Georgii 1980, Krug 2001, Wagenknecht 1996).

Modeling and Simulation Techniques

The simulation model was implemented by using the simulation software RAMSES version 3.0.1 b5 [Fischlin, 1994; http://www.ito.umnw.ethz.ch/SysEcol/SimSoftware/SimSoftware.html]. RAMSES is based on MacMETH, the "Fast Modula-2 Language System For the Macintosh" (Wirth et al. 1992). The model dynamics were formulated as a mixed model which consisted of two parts: a system of partly coupled, continuous time differential equations (DESS - Differential Equation System Specification) and a discrete event system specification (DEVS - Discrete Event System Specification) (Fischlin et al. 1994). In a DEVS model any change is formulated as an instantaneous state transition function (Fischlin et al. 1994), which lends itself well for the modeling of switches between behavioral modes or states of individual animals.

The vegetation was modeled by a DESS with a time step of 1 day. Within a given vegetation type, all variables were calculated as global means, regardless of the specific location of the vegetation patch (50x50m). This means the vegetation model is a classical population model and is different from the individual based nature of the other parts of the model.

The variables which describe the state of an individual deer were calculated for every single individual separately: Body weight was modeled by a DESS with a time step of 1 day; the intake of dry matter of the phytomass and the energy intake were calculated by a DEVS. Output variables, which describe the state of the deer population, were calculated as means from the set of currently present individuals. Thus sample size depended on the assumed deer density.

Sensitivity Analysis

We did a qualitative sensitivity analysis by varying the following model parameters within their value range as observed in the study site: mean duration of single rumination bout and date when the deer enter the park.

Results

The Model

MODEL STRUCTURE

The simulation model consisted of four distinct submodels (Fig. 1):

The vegetation submodel simulates the daily changes of phytomass quantity and quality for four different vegetation types: subalpine grasslands, subalpine meadows, alpine meadows, and subalpine forests. Vegetation growth was modelled as logistic and the vegetation quality was assumed to depend linearly on current vegetation quantity.

<Insert Figure 1 here>

The foraging submodel simulates phytomass and energy intake. Energy intake was constrained by the time needed for foraging and digestion.

The physiology submodel simulates the weight changes of every individual deer based on the energy intake and the daily energy requirements. Calculated energy requirements were dependent on the season, activity, and the sex of the animal.

The movement submodel simulates the use of a particular habitat. It was assumed animals switch twice per day among two vegetation types, e.g. between a grassland and a forest. Four different alternatives on how deers use their habitat were modeled: a switch between either subalpine grassland or subalpine meadow use during the night and forest use during the day, a switch between alpine meadow during the day and subalpine grassland use outside the park during the night, or a 24 hour use of alpine grassland.

Every deer has been modeled as a separate individual. The body weight of stages was assumed to be 100 and that of hinds 70 kg at the start of a simulation.

FORAGING MODEL

Since ruminant grazers are constrained by the foraging rate and by the digestion rate (Fryxell 1991), we defined the foraging Constraint *C* (kg of Dry Matter /d) as the instantaneous intake of grass on a small-scale vegetation patch. In our model the momentary intake was only a function of cropping or grazing, not of searching. The foraging submodel assumed that no significant amounts of time are spent searching. Actual searching behavior was only simulated at the landscape level by the movement submodel (day by day movement within the summer home range).

This lead to a functional response of type II (Fryxell 1991, Spalinger & Hobbs 1992). Thus we used a Michaelis-Menten intake function. The basic assumption underlying this function was that cropping is only constrained by the mean bite size, and that bite size is constrained by the phytomass density (Spalinger & Hobbs 1992). Thus forage intake is a function of phytomass (V, kg DM/ha) and of time per day spent cropping or grazing (t_{graz}, day):

$$C = aV/(b + V) \qquad (1)$$

where a is the maximum rate of forage consumption per herbivore (kg DM/d) and b is the phytomass abundance (kg DM/ha) at which the consumption rate is half of the maximum. The following values were used (Fryxell 1991, Wickstrom et al. 1984):

$a = 0.12$ (kg DM/d)/W, $b = 500$ kg DM / ha

Digestion was modeled explicitly by assuming an exponential decay of rumen fill (Spalinger et al. 1986). It is determined by rumen capacity and by the mean digestion rate. It is therefore a function of Rumen Volume (RV, in kg ingested DM) and mean residence time of ingested forage.

RV scaled with the body weight of the deer (W, kg):

$$RV = 0.015W \tag{2}$$

Parameters were determined using weight data on ingested wet biomass as estimated for summer months and for moose (Moen et al. 1997). We adapted these data for red deer assuming the generally observed differences between intermediate grazers and concentrate selectors is also applicable in our case (Hofmann 1989, Robbins 1993). The conversion of wet biomass into rumen dry matter was estimated from Gasaway & Coady (1974) and Sibbald & Milne (1993). Elsden et al. (1946) and Illius & Gordon (1992) have measured a gut DM load of 2.2% of body weight for red deer, Illius & Gordon (1991) one of 2.1%. Rumen DM load varies greatly between summer and winter season. Winter DM capacity of rumen is up to 30% larger than in summer (Gasaway & Coady 1974, Moen et al. 1997). Since our model is applicable only to the summer, we therefore favored lower end values.

The exponential decay of rumen fill was formulated as this:

$$RF = e^{-t/MRT} \tag{3}$$

where Rumen Fill (*RF*) was measured as a percentage of *RV*. *RF* represents the momentary fraction of the rumen capacity, which is actually filled with ingested phytomass. The time *t* (d) is the length of one rumination period plus that of the preceding foraging period.

The Mean Retention Time (*MRT*, d) was assumed to be a function of forage quality, i.e. fiber content (*NDF*, percentage Neutral Detergent Fiber) (Spalinger et al. 1986):

$$MRT = -\,0.1655 + 0.124\mathrm{Ln}(NDF) \tag{4}$$

We assumed the switching of an animal between foraging and rumination would depend only on the actual rumen content (Wagner 1992). In the model a deer forages until *RF* equals *RV*.

The subsequent rumination period was parameterized using observed activity patterns. For instance, in a standard simulation run we assumed a rumination time of 2 h, similar to the value observed in undisturbed areas (Bützler 1991, Georgii 1980, Krug 2001). In the model forage quality can not influence the length of a rumination period. It can only limit the amount of forage an animal can actually digest per day by the variable *MRT*, that is the amount of free rumen space per day that can be refilled by food intake.

The daily ingested phytomass (kcal/d) needed to be converted into daily energy intake by using the Digestible fraction of Energy (*DE*, kcal/g) contained in the forage, or respectively the Metabolizable Energy (*ME*, kcal/g). To convert *DE* into *ME* we used the following formula (Moen et al. 1997):

$$ME = 0.96DE - 0.27 \qquad (5)$$

The difference between *ME* and *DE* accounts mainly for energy losses in urine and methane (Minson 1990, Moen et al. 1997).

PHYSIOLOGY MODEL

The energy requirements by deer were defined in terms of *ME*. Literature data on energy requirements are usually given merely as Net Energy requirements (*NE*). The difference between *NE* and *ME* accounts for energy losses due to inefficiencies in chewing, ruminating, and digesting, which result in heat losses (Minson 1990, Moen et al. 1997). We modeled different efficiencies for maintenance/respiration (k_m), lactation (k_l), fattening/growth (k_f), and gestation (k_g). The latter is the efficiency by which the fetus converts energy into body weight. The following parameterization was used in the model:

k_m = 0.7 (ARC 1980, Moen et al. 1997, Robbins 1993)

k_l = 0.65 (ARC 1980, Moen et al. 1997)

k_f = 0.45 (Moen et al. 1997, Robbins 1993)

$\mathrm{k_g}$ = 0.15 (Robbins 1993)

For k_m and k_l we chose the upper values found in the cited literature.

The energy requirements per day were calculated as the sum of Basal Metabolic Rate (*BMR*), the activity specific loss, plus the reproduction needs in case of a hind. The net balance between daily energy intake and the energy requirements could then be calculated as a change in weight:

$$BMR = 1.43 * 41.76 \text{ (kcal/d)}/W \qquad (6)$$

The activity specific energy requirements for standing (*ES*), for foraging (*EF*) and for walking (*EW*) were calculated as follows:

$$ES = 1.43 * T_s * 10.56 \text{ (kcal/d)}/W \qquad (7)$$

$$EF = 1.43 * T_f * 9.0 \text{ (kcal/d)}/W \qquad (8)$$

$$EW = 1.43 * S_w * 0.68 \text{ (kcal/d)}/W \qquad \text{(stags)}$$

$$EW = 1.43 * S_w * 0.8 \text{ (kcal/d)}/W \qquad \text{(hinds)} \qquad (9)$$

(7) and (8) were taken from (Fryxell 1991). T_s is the portion of a day an animal spends standing (d) and T_f that it spends foraging (d). Equation (9) was taken from (Parker et al. 1984), where S_w is the daily walking distance of a deer in km. We assumed for S_w 2 – 3 km per day.

We calculated the energy requirements for gestation per day (E_g) from the energy content (E_f) within the fetus as given by its weight (W_f).

$$E_f = 6.667 * 1000.0 \text{ kcal/kg (derived from Robbins 1993)} \qquad (10)$$

We assumed a fixed ratio of 0.094 (Geist 1998) between the body weight of the mother and that of the newborn calf. The growth of the fetus was modeled exponentially (Bubenik 1984). The gestation time was assumed to be 238 days and in a standard simulation run simulated births happened on the 30th May. Thus we could calculate E_g as a function of the gestation time (T_g) and of the body weight of the mother at birth (W_m):

$$E_g = 2E_f(0.094\, W_m /(238)^2)T_g \text{ kcal/d} \qquad (11)$$

The energy requirements for lactation (E_l) were parameterized after Clutton-Brock et al. (1982):

$$E_l = \quad 2857 \text{ kcal/ d (day 1 – 50 of lactation)}$$

$$2857 - 17.15 * t \text{ kcal/ d} \quad (\text{day } 51 - 175) \qquad (12)$$

Daily weight changes were calculated on the basis of the energy balance. Energy content of body tissues in *ME* was assumed to be 2.22*5270 kcal/kg (Robbins 1993). From this followed the change in weight per energy intake (W_{Change}):

$$W_{Change} = 0.000085 \quad \text{kg/kcal} \qquad (13)$$

VEGETATION MODEL

The vegetation submodel calculates the changes in forage quantity (*V*) and quality (*NDF*, *DE*) during summer. We assumed logistic growth and that forage quality (*NDF*, *DE*) were both formulated as inverse, linear functions of phytomass quantity (Fryxell 1991, Van der Wal et al. 2000).

The vegetation was classified into four vegetation types (Zoller 1995): subalpine grassland, subalpine meadow, alpine meadow and subalpine forest. Within the study area the subalpine grassland was restricted to a single patch of 10 ha. We assumed subalpine grassland to be dominated by *Trisetetum flavescens* L, subalpine meadows by *Festuca rubra* L. (Schütz et al. 2000), alpine meadows by *Seslerio-Caricetum sempervirentis* (Zoller 1995), and subalpine forest by *Pinus silvestris* L.

Growth parameters were derived from two sampling points early and late in summer. Data for subalpine grassland and subalpine meadows were taken from Holzgang (1997), those for alpine meadows from Filli et al. (1994), and those for forests from Jens-Peter Kiel (2000, unpublished data; Küffer, 2000). Initial phytomass at the beginning of the growing season was assumed to be 500 kg/ha for all vegetation types (Filli, pers. comm.). Dates for the begin and end of the growing season were provided by Filli (unpublished data).

DE was calculated from crude protein content (Minson 1990), and *NDF* from crude fiber content (Van Soest 1994):

$$V = rV(K-V)/K \qquad (14)$$

$$DE = DE_0 - a_{DE}*V \qquad (15)$$

$$NDF = NDF_0 + a_{NDF}*V \qquad (16)$$

<Insert Tables 1a – 1d here>

MOVEMENT MODEL

The use of the habitat was not modeled spatially explicitly. From behavioral studies (Filli, unpublished data) we defined four kinds of habitat uses:

Type 1 (Il Fuorn type) switches daily between subalpine grassland and subalpine forest. These animals have been observed to feed on open subalpine grasslands during the night and due to disturbances to retreat to the subalpine forest during the day.

Type 2 (Stabelchod type) resembles Type 1 but during the night feeds on subalpine meadows.

Type 3 (Margunet type) stays on alpine meadows day and night.

Type 4 (Val Foraz type) switches between alpine meadow (day) and subalpine grassland (night).

For all four types we assumed that the animals switch their behavior every 12 hours.

DISCUSSION OF SIMULATION RESULTS AND MODEL VALIDATION

Grazing on subalpine grassland with optimal phytomass availability (3'000 – 4'000 kg/ha) at the end of the growing season leads to a daily intake of ca. 4 kg/d for a 100 kg stag and 2.8 kg/d for a 75 kg hind (Fig. 2). 3 kg/d for a 100 kg stag and 2.1 kg/d for a 70 kg hind are given in the literature as upper limits of daily intake by red deer (Bützler 1991, Wagenknecht 1996). Thus, the simulated intake per day is about 25% higher than value found in the literature (Bützler 1991, Wagenknecht 1996). This indicates that the constraining digestive rates we chose were rather high, yet, this is without effect on the main results.

<Insert Figure 2 *here>*

In the simulation the animals spent ca. 30% of their time feeding and ca. 70% ruminating. Actually observed activity patterns have indicated a substantially higher day time activity (65% active Georgii 1980, Krug 2001). This indicates that the modeled digestive constraints are high relative to the availability constraints.

On subalpine grassland simulated stags gained about 35% weight during the growing season. From park data on weight loss in winter, on rut and on observed growths a weight gain of ca. 30% should be expected (Blankenhorn et al. 1979, Clutton-Brock et al. 1982). A hind with a calf gains ca. 5% of body weight during the growing season. Weight losses during winter are expected to be ca. 25% (Blankenhorn et al. 1979). Thus, the model indicates that hinds can gestate and lactate only every second to third year or would suffer a negative energy balance.

Food Availability Versus Digestive Constraints

Optimal foraging theory emphasises the question whether and under which conditions food availability or digestion is constraining maximal daily energy intake. In agreement with several other studies we found that food availability is constraining energy intake only at very low levels of phytomass densities. Above that level the time needed for digestion and thus the quality not the quantity of phytomass determines mainly daily energy intake (Bergman et al. 2001, Fryxell 1991, Wilmshurst et al. 1999).

In our simulation maximum daily energy intake was observed within the range of 800 – 1'200 kg phytomass dry matter per hectare (Fig. 3). Below ca. 500 kg DM/ha animals need more time to forage than to digest, above this level they need more time to digest than to forage. Thus, our results confirm that optimal phytomass availability is attained at a relatively low level of phytomass density and that during most of the growing season, digestion rather than food availability is constraining.

<Insert Figure 3 *here>*

Human disturbances which lead to a pronounced irregularity of the activity pattern and thus to an increase of mean rumination bout length (Bützler 1991) result also in a smaller daily energy intake and in a shift from availability towards digestion constraints. We concluded that an explicit modeling of the digestion constraint, even if modeled in a very simple way as in our study, reveals important interactions between activity patterns and daily energy intake.

The model shows that digestive rather than availability constraints affect red deer in the SNP. Only in the forest during early growing season and under conditions of overgrazing may the food availability play a substantial role. This is in accordance with modeling results by Fryxell (1991).

Does Summer Food Availability Regulate Population Size?

Regulation of population size as simulated by the model shows major non-linearities. Because of the little sensitivity of daily intake at large phytomass densities (> 1'000 kg/ha), forage scarcity is significant for red deer only at very low phytomass abundances. At those low levels the ratio of red deer by phytomass densities leads to an accelerated, complete depletion of the grassland. In particular we noted the following three facts:

Firstly, high phytomass quality and low phytomass quantity during early growing season, lead to a situation where food availability constraint becomes more important than digestion constraint .

<*Insert Figure* 4 *here*>

Secondly, at low phytomass quantity absolute quantitative impact due to forage uptake by deer is highest.

Thirdly, per capita energy requirements for hinds are highest in the early growing season.

Taking into account that regulation affects calves first and thus population regulation is characterized by a time delay of several years (Saether 1997), a population regulation dominated by food availability would lead to completely depleted grassland for several years before population size would start to respond.

From all this we concluded that mean summer food availability has little effect on deer densities.

Carrying Capacity and Population Regulation

If deer enter the park at 15th May (Il Fourn Behavior type) the resulting carrying capacity was 11.5 deer/ha subalpine grassland, if they entered 5 days later, 25 deer/ha were observed. It appears the carrying capacity is very sensitive to the date when the animals enter the park.

This coincides with the time when the grassland is most sensitive to overgrazing. Overgrazing in this early period cannot be compensated during the subsequent growing season if grazing pressure stays high.

Up to the present estimates of the carrying capacity of the Swiss National Park have been derived from annual productivity and mean per capita energy consumption. However, since the early growing season appears to form a bottleneck, such estimates have to be questioned.

Finally, should the found sensitivity to only slight changes in phytomass quantity in spring be real, we would expect high deer densities to react sensitively to the interannual variability in the begin and end of the growing season and the particular conditions affecting productivity in spring, i.e. to be sensitive to stochastic environmental variability.

This means that the effect of climate change on the growing season may dramatically influence the carrying capacity.

Conclusions

Consistent with previous results we found that food quality normally limits daily energy intake by red deer, whereas food quantity limits it only under very rare conditions, i.e. at very low phytomass densities. This fact confirms that the model captures correctly relevant features of the real situation in the field. Due to the reverse relationship between the phytomass quality and quantity growth of phytomass simultaneously increases phytomass availability and decreases phytomass quality. This leads in the model to an optimal phytomass at intermediate levels.

The high sensitivity to the mean length of a single rumination bout indicates that daily energy intake may also strongly influenced by changes in behavior. For instance an irregular activity pattern due to human disturbances leads to a lower daily energy intake. This indicates a mechanism by which human disturbances influence the condition of red deer even during summer months.

The results indicate that deer populations are not regulated due to food scarcity during summer months. Thanks to the relationship between digestion and food availability only very low phytomass densities have the potential to influence deer condition and thus fitness and in the longer term also population size. However, under these conditions a heavy overgrazing would have to be expected, which would lead to the collapse of the system. Since such critical interactions between vegetation and a red deer population occur only in early spring, any estimate of a carrying capacity, which is based on a mean seasonal productivity may have to be distrusted.

The identified high sensitivity to phytomass availability in the early growing season indicates that any changes in the begin of the growing season or changes in the exact date in spring when the deer enter the park may affect the state of the grasslands in the Swiss National Park, i.e. whether they are overgrazed or not.

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Figure Legends

Fig. 1: The basic structure of the simulation model: The vegetation submodel calculates phytomass availability (*V*, kg DM/ ha) and quality (Neutral Detergent Fiber *NDF*, Digestible Energy *DE*). The foraging submodel calculates the energy intake (a) and the influences by animal foraging on the vegetation (b). Based on the balance between energy intake(c) and physiological needs the physiology submodel calculates daily bodyweight changes. The movement submodel allows animals to choose on which vegetation type to forage.

Fig. 2: The standard simulation run covers 150 days, i.e. the time the animals remain in the summer range within the park, and starts from a density of 1 deer/ha. Consumed phytomass kg DM/d (solid line); portion of day spent feeding (dashed line); bodyweight change (hashed line) (kg DM/ha).

Fig. 3: Energy (kcal/d) and food consumption (kg DM/d) as a function of phytomass availability (kg/ha): portion of day spent feeding (dashed line), spent ruminating (hashed line); daily energy intake (dotted line)**.**

Fig. 4: Four different simulation runs for deer population densities of 28 animals / 4 ha, 30/ 4ha, 31/ 4 ha, 32 / 4 ha (from top to bottom) with a mean weight out of a population of 50% stags and 50% hinds. Bodyweight (dashed line); phytomass abundance (kg

DM/ha) on subalpine grassland (solid line).

Figure 1:

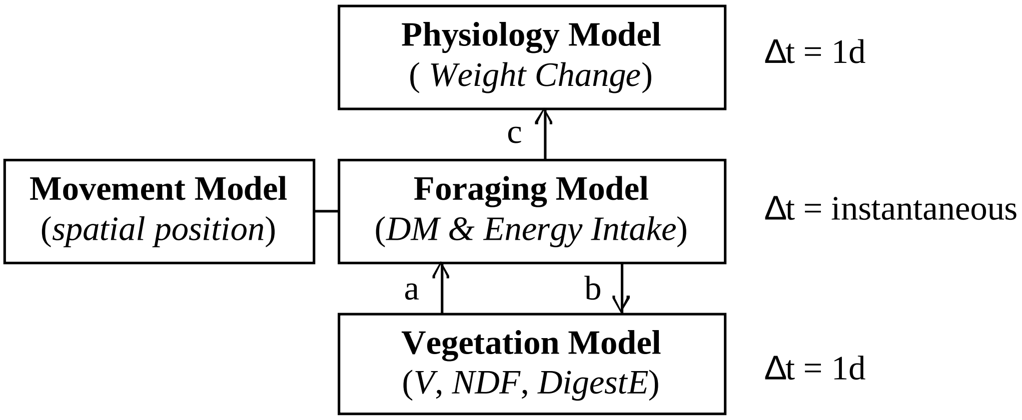
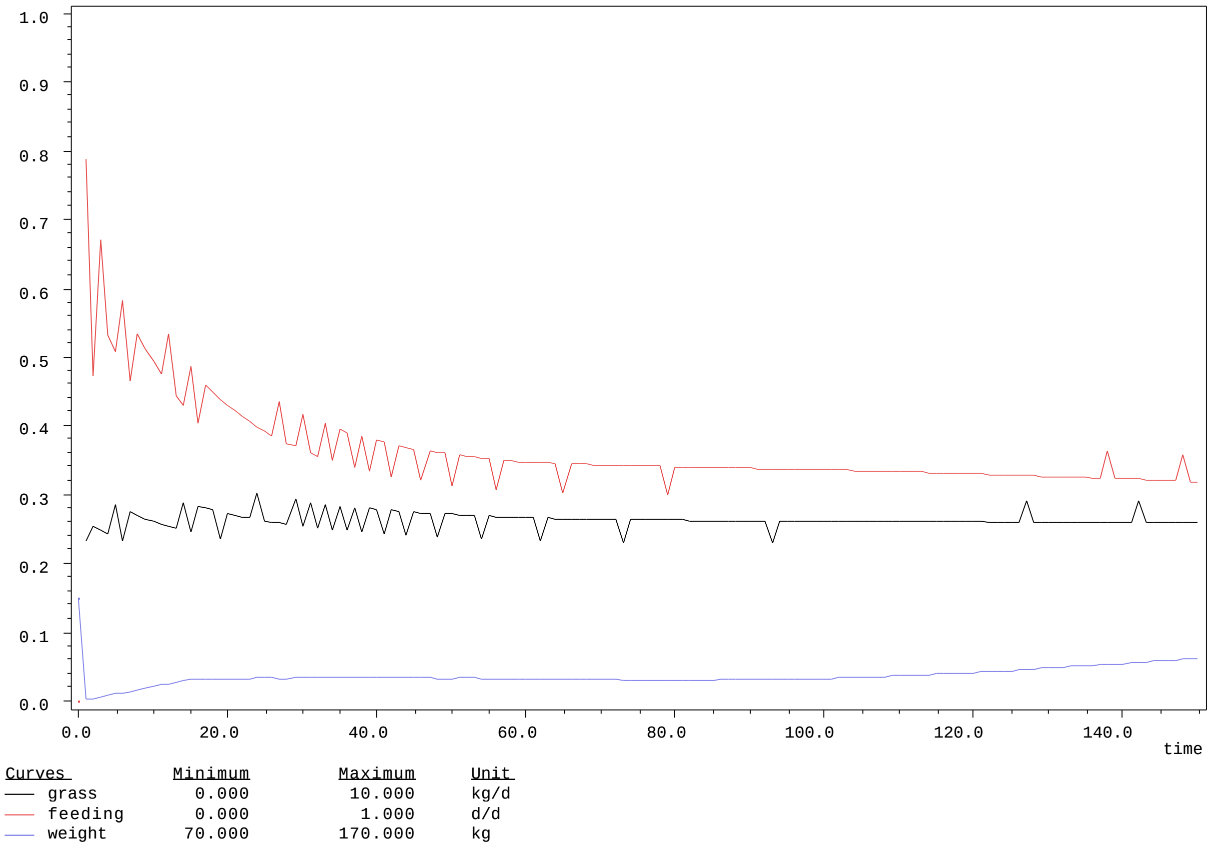

Physiology Model
(Weight Change)
Δt = 1d
c
Movement Model
(spatial position)
Foraging Model
(DM & Energy Intake)
Δt = instantaneous
a
b
Vegetation Model
(V, NDF, DigestE)
Δt = 1d

Figure 2: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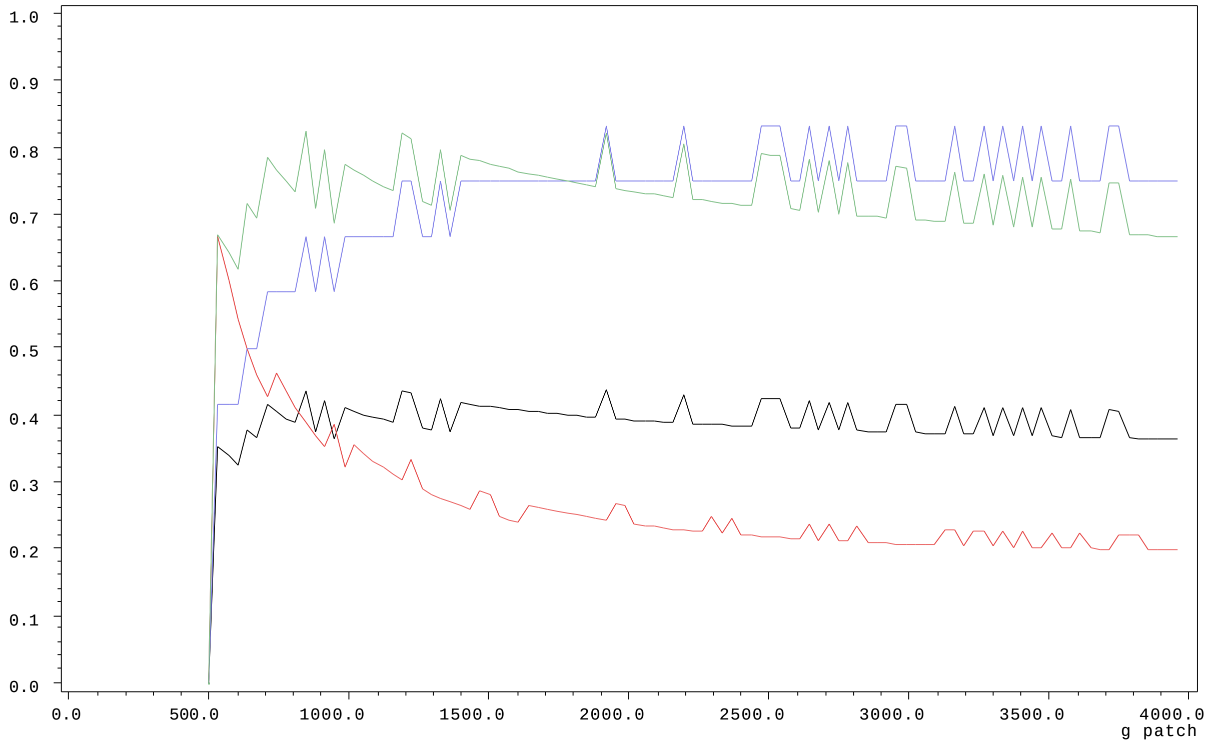
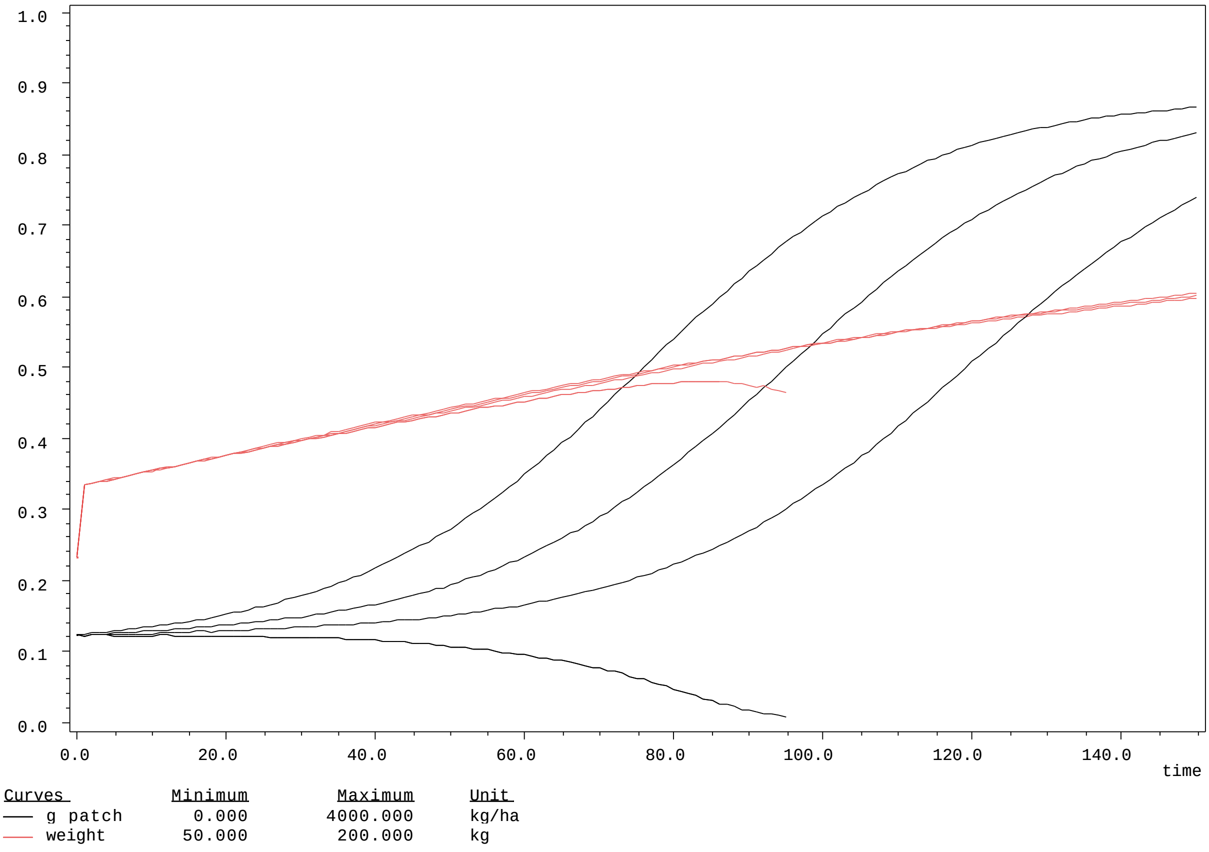
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.0
20.0
40.0
60.0
80.0
100.0
120.0
140.0
time
Curves Minimum Maximum Unit
grass 0.000 10.000 kg/d
feeding 0.000 1.000 d/d
weight 70.000 170.000 kg

Figure 3:



Curves		Minimum	Maximum	Unit
—	grass	0.000	10.000	kg/d
—	feeding	0.000	1.000	d/d
—	ruminati	0.000	1.000	d/d
—	energy	0.000	15000.000	kcal/d

Figure 4:


1.0
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0.1
0.0
0.0
20.0
40.0
60.0
80.0
100.0
120.0
140.0
time
Curves
g patch
weight
Minimum
0.000
50.000
Maximum
4000.000
200.000
Unit
kg/ha
kg

Table 1a

Definition	value	symbol
vegetation start	15th of May	t_{0Grass}
vegetation end	12th of October	t_{1Grass}
NDF at t_{0Grass}	44.5 %	NDF_{0Grass}
growth rate	0.068 d^{-1}	r_{Grass}
DE at t_{0Grass}	3.25 kcal/g	DE_{0Grass}
change rate of NDF	0.0036 %/kg DM	$a_{NDFGrass}$
change rate of DE	0.00003 (kcal/g)/kg DM	$a_{DEGrass}$
carrying capacity	3960 kg DM/ha	K_{Grass}

Tab. 1a: Parameters of the submodel “subalpine grassland”.

Table 1b

Definition	value	symbol
vegetation start	15th of May	$t_{0SubalpMead}$
vegetation end	12th of October	$t_{1\ SubalpMead}$
carrying capacity	2870 kg DM/ha	$K_{\ SubalpMead}$
growth rate	0.061 d^{-1}	$r_{\ SubalpMead}$
DE at $t_{0SubalpMead}$	3.12 kcal/g	$DE_{0\ SubalpMead}$
change rate of DE	0.000025 (kcal/g)/kg DM	$a_{DE\ SubalpMead}$
NDF at $t_{0SubalpMead}$	47 %	$NDF_{0\ SubalpMead}$
change rate of NDF	0.0036 %/kg DM	$a_{NDF\ SubalpMead}$

Tab. 1b: Parameters of the submodel “subalpine meadow”.

Table 1c

Definition	value	symbol
vegetation start	15th of June	$t_{0\ AlpMead}$
vegetation end	15th of September	$t_{1\ AlpMead}$
carrying capacity	1170 kg DM/ha	$K_{AlpMead}$
growth rate	0.041 d^{-1}	$r_{AlpMead}$
DE at $t_{0\ AlpMead}$	3.04 kcal/g	$DE_{0\ AlpMead}$
change rate of DE	0.0 (kcal/g)/kg DM	$a_{DE\ AlpMead}$
NDF at $t_{0\ AlpMead}$	45.6 %	$NDF_{0\ AlpMead}$
change rate of NDF	0.0 %/kg DM	$a_{NDF\ AlpMead}$

Tab. 1c: Parameters of the submodel “alpine grassland”.

Table 1d

Definition	value	symbol
vegetation start	15th of May	$t_{0\ Forest}$
vegetation end	12th of October	$t_{1Forest}$
carrying capacity	715 kg DM/ha	K_{Forest}
growth rate	0.022 d^{-1}	r_{Forest}
DE at $t_{0\ Forest}$	3.12 kcal/g	$DE_{0\ Forest}$
change rate of DE	0.00028 (kcal/g)/kg DM	$a_{DE\ Forest}$
NDF at $t_{0\ Forest}$	47 %	$NDF_{0\ Forest}$
change rate of NDF	0.034 %/kg DM	$a_{NDF\ Forest}$

Tab. 1d: Parameters of the submodel “subalpine forest”.