A herbivore specific grazing capacity model accounting for spatio-temporal environmental variation: A tool for a more sustainable nature conservation and rangeland management

A. Ebrahimia, T. Milotic, M. Hoffmann

1. Introduction

Grazing with livestock is a common feature of nature and rangeland management. Although both aim at different, seemingly opposing goals, i.e. maintenance of biodiversity values versus maximization of animal production, they nonetheless have a common interest in maintaining the rangeland or natural environment in a state that ensures either the first or the second goal. In order to accomplish an effective and efficient grazing management, in terms of grazer density, grazer composition, grazing seasonality, and to prevent under- and overgrazing, a grazing capacity model (GCM) was developed, that should be applicable in both rangeland and nature conservation management conditions and that takes spatio-temporal environmental variation into account. This spatio-temporally dynamic model considers crucial variables at both the terrain and the grazer level, such as (seasonally) fluctuating forage yield, forage quality, plant palatability, accessibility of the area, soil erosion vulnerability, animal nutritive requirements, animal behaviour and general habitat condition. It predicts the optimal grazer species and density, taking into account the seasonal variation in animal needs and fluctuating terrain characteristics. A sensitivity analysis was conducted to define each parameter’s relative impact on the final outcome of the model.

We present the GCM outline and illustrate the functionality of this model for Shetland ponies and Highland cattle, grazing in a temperate coastal dune environment. According to the model, seasonal fluctuations in optimal grazer densities occur: the area can support higher densities in summer and autumn than it can during winter and spring. With the current density of grazing animals and the choice for year-round grazing at non-fluctuating animal densities, the model consequently predicts overgrazing in winter and undergrazing in summer and autumn. Both undergrazing and overgrazing scenarios might lead to non-sustainable situations in the future.

1. Introduction

Grazing as a management tool in nature reserves and rangeland has little aims in common. In nature reserves it generally aims at maximizing or optimizing biodiversity values, whereas in rangeland, it primarily aims at maximizing animal production. Nonetheless, both share the need for sustainability, maintaining a certain level of ecosystem stability. In both cases this is primarily driven by grazer pressure, grazer composition and grazing regime (e.g. year-round against seasonal grazing).

It is generally accepted that low to moderate grazing intensities of large herbivores create spatially heterogeneous landscapes (van Oene et al., 1999; Olff et al., 1999), which is driven by selective feeding behaviour and differential habitat use of the herbivores. It affects vegetation succession by the removal of tall, dominant plant species (such as tall grasses and shrubs) (Fuhlendorf and Engle, 2004). Well-adapted grazing densities stop the expansion of late-successional or invasive plant species, which ultimately results in higher biodiversity and a structurally more heterogeneous landscape (van Oene et al., 1999). These are the principle mechanisms for nature conservation management. Rangeland management, on the other hand, is frequently confronted with non-sustainable overgrazing regimes, leading to deterioration of vegetation, increased soil erosion (Fleischner, 1994; Sansom, 1999), lowered biodiversity (Sansom, 1999). In the end, general rangeland deterioration and decreased animal production might be the result (e.g. Danckwerts and King, 1984; Friedel, 1991).

Hence, a proper estimation of the grazing capacity and its primarily season-driven dynamics is crucial in order to accomplish an effective and efficient grazing management for nature conservation.
purposes as well as an optimal long-term animal production level for rangeland purposes, rather than a short-term maximal animal production. In both cases a certain level of vegetation development should retain in order to leave the aimed semi-natural landscape intact or to keep the animal productivity level of the rangeland landscape optimal in the long term. We therefore developed a grazing capacity model that should be applicable for both nature and rangeland managers. It differs significantly from other grazing models in nature conservation, that depart from specific flora or fauna characteristics (e.g. Cousins et al., 2003; Pöyry et al., 2005; Schröder et al., 2008; Wintle et al., 2005) or from more general management approaches (e.g. Rudner et al., 2007). Our approach departs from the assumption that rangeland and nature conservation management goals in the end show important similarities, allowing to treat grazing capacity from the same angle, i.e. specific management goals combined with animal needs and impact. Nevertheless, aforementioned nature conservation aimed model approaches might enable further tuning of management goals in our model.

Grazing capacity (GC) here refers to the optimum animal population density (instead of the maximum density) that a particular area can sustain over a long time span (Holechek et al., 2004). More precisely, we follow a recent definition used in rangeland management (SRM, 1998), i.e. grazing capacity is "the optimal number of (a combination of) livestock (and/or wildlife) that may be maintained sustainably on a management unit as far as compatible with management objectives for that unit". Hence, grazing capacity is not merely concerning site and herbivore characteristics, but also refers to specific management goals. As grazing capacity is well below the herbivore number that causes die-offs, destruction, or even negative trends in resources, including habitats, soils and the complete ecosystem, the above given rangeland management concept of grazing capacity is perfectly applicable in nature conservation management as well.

Despite the obvious importance of the determination of grazing capacity in nature conservation and rangeland management, existing methods depend more or less on trial and error (Valentine, 2001; Smith, 2003), and those that are developed to estimate grazing capacity are generally referring to rangeland conditions. All of them are either not evidence-based, or site-specific and hence inapplicable in other situations, or focused on short-term agricultural gain (e.g. Bosch and Boosyen, 1992a,b; Kohthmann and Himmant, 1992; Steenekamp and Bosch, 1995). More advanced models incorporate forage mass and nutritional characteristics of plant species and habitats as well as the grazer nutrient requirements (Hobbs et al., 1982; Hobbs and Swift, 1985). Still other models are specifically designed to estimate wildlife carrying capacity based on forage availability and relate it to population growth (Mclead, 1997) and to foraging behaviour alteration due to changing population size (Morris and Mukherjee, 2007). The models developed by Holechek (1988) and Holechek et al. (2004) include already forage yield and total usable forage by incorporating a proper use factor or correction for allowable use (called a "harvest coefficient", correcting for habitat condition and specific management objectives), forage demand of herbivores and adjustments for slope and distance from water supplies. But the latter approach still neglects some crucial parameters, such as forage quality, species specific animal nutrient requirements, habitat condition, plant palatability and landscape barriers, such as relative inaccessibility of habitats, and neglects spatio-temporal variation in environmental conditions. It therefore still tends to overestimate grazing capacity, when the general goal is to maintain animals and habitats in a long-term sustainable condition.

Therefore, we developed a model that includes all these additional determinants of GC into Holechek's original concept in order to adapt his primarily rangeland directed GC model for a more general use in both nature conservation and rangeland management.

As the workability of a model decreases with an increasing number of parameters, the relevance of all input parameters in the final GC output was determined with a sensitivity analysis. After this analysis, one might be able to simplify the model up to a level that needs as little as possible parameters to be measured or estimated.

The proposed model aims to be an accurate tool in nature conservation as well as sustainable rangeland management and should be generally applicable in spatially heterogeneous landscapes with seasonally and yearly fluctuating forage yield and nutrient availability.

Specific research questions raised are:

- Can a generally applicable GC model be developed that considers all relevant GC determinants and that enables optimization of nature conservation management or sustainable rangeland management, and can the number of model parameters be limited?
- Is optimal grazer density fluctuating among seasons and years?
- Is knowledge of the forage yield, or accessible and available phytomass in the area, sufficient to estimate grazing capacity accurately, or is its nutritional quality, such as crude protein content or (digestible) energy, of additional relevance?
- What can we learn from a case study in a temperate coastal dune area with nature conservation goals to evaluate the model?

2. Materials and methods

2.1. Model description

The model incorporates both terrain characteristics and herbivore needs. On the one hand, it includes terrain accessibility, forage yield, harvest coefficient and forage quality traits and on the other hand animal nutritional requirements (Fig. 1 and Table 1). A general description of model subroutines is given hereafter. A more detailed description of the model is given by Ebrahimi (2007).

2.1.1. Accessibility of forage for livestock

Some parts of an area with potentially edible phytomass might be inaccessible to herbivores because of natural barriers such as steep slopes, water supply distances (Holechek, 1988), rock outcrops (Milchunas and Noy-Meir, 2002), dense surrounding, inedible and inaccessible scrub and other land use restrictions. In this model, the accessible area is calculated by Eq. (1) (Table 1), incorporating reduction coefficients for scrub hindrance (RCsh), steep slopes (RCsl) and water supply distance (RCwd) (Table 2).

2.1.2. Forage use defined by palatability index or harvest coefficient

In order to avoid overestimation of GC, forage quantification should be based on those plant species that really contribute to the grazer’s diet and not on all plant species present. When departing from the animal needs, a palatability index should be incorporated in the model, providing a GC contribution correction based on the specific preference of the herbivore itself. Using a palatability index has an effect on the total harvestable phytomass, according to the animal preference and capability of foraging the total available phytomass. In the case study, we estimated the palatability index using observational data of diet preference of the considered herbivore species (Lamoot et al., 2005). Diet preference is derived from Jacobs’ index of selection (Di) (Eq. (3), Table 1) (Jacobs, 1974) and is expressed with values ranging from −1 to +1, with negative and positive values indicating avoidance and preference, respectively. As the palatability of plants was assumed to be correlated with animal diet preference, the palatability index (Pi) was
defined using the diet preference index \( (D_i) \). The range of the diet preference index was split into five classes with equal 0.4 interval size to which a palatability index \( (P_i) \) was assigned: 

- \([1;0.6] D_i \) (strong preference) corresponds with 100% \( P_i \),
- \([0.6;0.2] D_i \) (preference) with 75% \( P_i \),
- \([0.2;−0.2] D_i \) (indifference) with 50% \( P_i \),
- \([-0.2;−0.6] D_i \) (avoidance) with 25% \( P_i \),
- \([-0.6;−1] D_i \) (strong avoidance) corresponds with 0% \( P_i \).

Ultimately, these diet preference classes were transformed into Eq. (4) (Table 1) using S Plus 6.2 for Windows.

The opposite approach is the one from the managers' point of view, i.e. which part of the phytomass is allowed to be foraged without endangering management goals? To do so, a harvest coefficient \( (HC) \) is assigned to each habitat. This coefficient should assign a part of the current herbage production \( (1) \) to consumption by wildlife other than the introduced grazers (e.g. deer, lagomorphs, rodents, insects and other invertebrates) or trampling by the large herbivores; (2) to protection of plant vigour, reproduction and regrowth at habitat level; and (3) to maintenance of a certain stubble height for soil conservation purposes and proper functioning of the system. From research on the grazing induced root-growth cessation of perennial grasses (e.g. Dietz, 1989; Lamman, 1994), a general 50% HC was deduced, which is applicable in ideal situations, i.e. in entirely healthy habitats, with a soil surface resistant to erosion and key species relatively tolerant to grazing. In case of less ideal situations, reductions should be made according to habitat condition, soil erodibility, required stubble height and management objectives (Eq. (5), Table 1).

A decision on the total accessible and available forage for the introduced herbivores is made, comparing palatability and harvest coefficient values, taking the most conservative one (lowest one) as an input to the model.

### 2.1.3. Forage characteristics and animal food requirements

Both quantity and quality of food resources are subject of spatio-temporal variation, because of the inter-annual or seasonal variation of yield affecting factors (e.g. weather conditions and ground water level). Assigning a given proportion of forage to animal consumption without considering its quality is therefore inappropriate. Hence, animal requirement and subsequently GC should be derived from forage yield as well as nutritive value of forage (Off et al., 2002). Crude protein \( (CP) \), energy and mineral content are widely accepted forage quality determinants (Baars, 2002; Beck and Peek, 2005; Beck et al., 2006; Cakmakci et al., 2004; FAO, 1991; Stoddart, 1960). Since energy and protein levels are often limiting determinants in (semi-)natural landscapes and minerals can easily be furnished to animals as supplements, we consider crude protein and energy (expressed as digestible, metabolizable or net energy) as the two main constraints of livestock nutritional requirements. Nevertheless, GC can also be determined by other forage nutrient parameters (e.g. fibre content, carbohydrates, vitamins), using the same model. Again, as in the case of palatability versus harvestability, GC is finally decided upon, taking the lowest allowable grazer density, according to the model outcomes using the different forage quality and quantity characteristics.

Grazing capacity is expressed as the number of animal units that can sustainably be nourished within a certain management unit. We consider an animal unit \( (AU) \) as a unit of animal nutrient demand or potential forage intake. The mean body weight of the predominant grazer species is used as the basis of the determination of an AU. Subsequently, the need of 1 AU for nutrients (e.g. protein, energy) and forage bulk is evaluated, considering the animal characteristics (e.g. kind, class, and breed), physio-
Table 1
Main equations of the model determining the accessible area, forage yield, palatability index, harvest coefficient, forage quality and grazing capacity.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Accessible area</td>
<td>( A_{aij} = (H_a - NGlu_i) \ast RCsl_i + RCsl_j^* \ast RCwd_j ) (1)</td>
</tr>
<tr>
<td>Forage yield</td>
<td>( FY_i = \sum_{i}^{n} FQ_i ) (2)</td>
</tr>
<tr>
<td>Diet preference</td>
<td>( D_i = (P_i + A_i) - (2 \ast P_i + A_i) ) (3)</td>
</tr>
<tr>
<td>Palatability index</td>
<td>( Pi = (-12.08 + D_i^2) + (61.717 + D_i) + 50 ) (4)</td>
</tr>
<tr>
<td>Harvest coefficient</td>
<td>( HC_i = HC_W + RC_G + RC_mo + RC_sth + RC_se ) (5)</td>
</tr>
</tbody>
</table>

Steps in the calculation of grazing capacity

- **Total accessible forage yield**
  \( FY_{aij} = A_{aij} + FY_i \) (6)
- **Total accessible and available forage yield**
  \( FY_{aij} = Min(PL, HC_i) + FY_{aij} \) (7)
- **Total accessible and available nutrients**
  \( TotFQ = \sum (FY_{aij} + FQ_{ij}) \) (8)
- **Total accessible and available forage yield**
  \( TotFY = \sum FY_{aij} \) (9)

**Grazing capacity**

- Based on forage yield
  \( GC_{fy} = \frac{TotFY}{FRB \ast GS} \) (10)

- Based on forage quality
  \( GC_{FQ} = \frac{TotFQ}{FQ_R \ast GS} \) (11)

- Digestible energy (equation adopted from NRC (1989) and applied in the case study)
  \( DE = 4.22 - (0.115 \ast ADP) + (0.0332 \ast CP) + (0.00112 \ast ADP^2) \) (12)

\* Variables: \( A_{aij} = \) total accessible area in the \( ij \)th habitat (ha); \( A_i = \) relative coverage of species \( i \) (%) ; \( ADP = \) acid detergent fibre (%); \( CP = \) crude protein (%); \( D_i = \) diet preference for species \( i \); \( DE = \) digestible energy (Mcal/kg); \( FRB = \) animal unit requirement for forage bulk (kg AU\(^{-1}\) day\(^{-1}\)); \( FQ_i = \) mean value of the considered forage quality parameter \( p = \) separately for protein, energy content, ...) of the \( ij \)th species (% DM or Mcal kg\(^{-1}\)); \( FQ_R = \) animal unit requirement for forage quality parameter \( p = \) kg AU\(^{-1}\) day\(^{-1}\); \( FY_{aij} = \) total accessible and available forage yield for the \( ij \)th species in habitat \( j \); \( FY_{aij} = \) total accessible forage yield for the \( ij \)th species in habitat \( j \); \( FY_i = \) mean forage yield of the \( ij \)th species in habitat \( j \); \( FY_i = \) forage yield of species \( i \) in quadrat \( q \) in habitat \( j \); \( FY_{aij} = \) forage yield of species \( i \) in quadrat \( q \) in habitat \( j \); \( HC_i = \) harvest coefficient for habitat \( j \) in optimal condition (%); \( HC_i = \) harvest coefficient for habitat \( j \); \( n = \) total number of plots containing species \( i \); \( NGlu_i = \) non-grazing land use of the \( ij \)th habitat (ha); \( Pi = \) area of the \( ij \)th habitat (ha); \( HC_W = \) general harvest coefficient for a habitat \( j \) in average condition (%); \( HC_i = \) harvest coefficient for habitat \( j \); \( n = \) total number of plots containing species \( i \); \( RCsl_i = \) relative coverage of species \( i \) (%) ; \( RCsl_i = \) relative coverage of species \( i \); \( RCwd_j = \) reduction coefficients for habitat \( j \)'s condition, management objectives, soil erodibility, scrub hindrance, slope, stubble height and water supply distance respectively (%); \( TotFQ = \) total accessible and available forage yield for the \( ij \)th species in habitat \( j \); \( TotFY = \) total accessible and available forage yield in the area (kg).

2.2. Case study

2.2.1. Study site

The model was applied on data gathered in a temperate coastal dune area along the Belgian-French border (51°4′45″N; 2°33′40″E), i.e. the Flemish Nature Reserve “De Westhoek”. Since 1997, a 60 ha large part of the nature reserve has been grazed by a fluctuating number of free-ranging Highland cattle and Shetland ponies. During the observation period within this particular study, 5 cattle and 8 Shetland ponies grazed the area, which corresponds to 0.08 and 0.13 AU ha\(^{-1}\), respectively. According to the indications given by Wallis de Vries et al. (1998), this should be considered as a relatively high grazing pressure compared to the assumed pressure in similar semi-natural grazing systems in temperate regions. Animal herds of both species remain in the study site year-round, and no additional food is supplied to the animals.

Six potentially grazed habitat types (i.e. plant communities with different species composition, cover and structure) were distinguished in the area: (1) dry grassland (co-dominance of Calamagrostis epigejos, Holcus lanatus and Festuca rubra with some other less prominent graminoids and forbs); (2) moist grassland (dominance of Agrostis stolonifera accompanied by some other more or less phreatophytic graminoids (e.g. Carex disticha, H. lanatus) and forbs (e.g. Mentha aquatica, Lythrum salicaria, ...)); (3) rush wetland (dominance of Juncus subnodulosus, C. disticha and A. stolonifera); (4) Calamagrostis grassland (absolute dominance of C. epigejos, other grasses and forbs were sparsely present); (5) scrub (co-dominance of Rosa pimpinellifolia, C. epigejos and larger scrub species (e.g. Hippophae rhamnoides and Prunus spinosa) with other grasses and forb species in the under storey); and (6) woodland (dominance of planted poplar trees along with other trees (e.g. Alnus glutinosa, Acer pseudoplatanus, ...)) with an abundant under storey dominated by ruderals like Calium aparine, Glechoma hederacea and Urtica dioica.

Following Dietz (1989) and Lamman (1994) the general 50% HC rule was applied to all habitats. Observational data of Highland cattle and Shetland ponies of Lamoot et al. (2005) were used to calculate diet preference values and corresponding palatability index values per plant species (Eqs. (3) and (4), Table 1). The accessible and available forage yield \( FY_{aij} \) per species and per habitat was deduced using the lower value of either harvest coefficient or palatability index (Eq. (7), Table 1).

Forage quantity and quality measures were conducted in each season during two consecutive years (spring 2004–winter 2005/2006). In each habitat type, forage quantity and quality traits were compared among seasons by a one-way ANOVA-test in Stata 8.

Grazing capacity was calculated for both Highland cattle and Shetland ponies as the sole grazer species in the area. The mean body weight of the Highland cows was set to 481 ± 21 kg (Lamoot et al., 2005) and was regarded as 1 animal unit (AU) for Highland cattle. Environmental conditions (topography, mean summer temperature of 16 °C), as well as animal characteristics (dry cow in maintenance, clean and dry coat of average thickness) were incorporated in the calculation of animal needs, using the NRC (2000b) program.
The nutritive demand of a Shetland pony with mean body weight of 205 ± 8 kg (considered as 1 animal unit for Shetland ponies) for digestible energy, crude protein and forage bulk was adopted from NRC (1989). Finally, grazing capacity of the total area was calculated for Highland cattle and Shetland ponies separately and compared to the current situation.

2.2.2. Parameter estimates

Several sources were used as input data in the model. Spatial data based on field mapping and aerial photography were used to calculate terrain accessibility. Field data were gathered in order to estimate forage quantity, quality (Ebrahimi, 2007) and palatability. Forage yield and forage quality data were gathered per habitat and species through several field work campaigns using a systematic-randomized sampling scheme (cf. Bonham, 1989).

Table 2

<table>
<thead>
<tr>
<th>Factor</th>
<th>Class</th>
<th>Reduction coefficient</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scrub hindrance (%)</td>
<td>0–60</td>
<td>0.0104x^2 + 0.6173x</td>
<td>FAO (1991)</td>
</tr>
<tr>
<td></td>
<td>&gt;60</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Slope steepness (%)</td>
<td>0–60</td>
<td>0.0093x^2 + 1.0409x</td>
<td>Holechek et al. (2004)</td>
</tr>
<tr>
<td></td>
<td>&gt;60</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>Water supply distance (km)</td>
<td>&lt;0.8</td>
<td>0</td>
<td>Holechek et al. (2004)</td>
</tr>
<tr>
<td></td>
<td>0.8 ≤ x ≤ 3.2</td>
<td>1.14x^2 – 7.1792x</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&gt;3.2</td>
<td>100</td>
<td></td>
</tr>
</tbody>
</table>

In Table 3, buffers with diameters of 800 and 3200 m were initially drawn around the digitized water pools. Furthermore, the buffer class 800–3200 m was split up into subclasses with a diameter of 200 m in order to calculate the reduction coefficient in this sensitive part of the equation (Table 2).

Table 3

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Forage yield (kg DM ha(^{-1}))</th>
<th>Crude protein (kg CP ha(^{-1}))</th>
<th>Digestible energy (Mcal ha(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Spring 2004</td>
<td>Summer 2004</td>
<td>Autumn 2004</td>
</tr>
<tr>
<td>Dry grassland</td>
<td>293 ± 78(a)</td>
<td>407 ± 78(ab)</td>
<td>739 ± 78(a)</td>
</tr>
<tr>
<td>Moist grassland</td>
<td>69 ± 83(a)</td>
<td>464 ± 83(bc)</td>
<td>618 ± 83(a)</td>
</tr>
<tr>
<td>Rush wetland</td>
<td>314 ± 119(a)</td>
<td>916 ± 90(a)</td>
<td>1189 ± 90(a)</td>
</tr>
<tr>
<td>Coloumgoristis</td>
<td>419 ± 81(ab)</td>
<td>623 ± 87(ab)</td>
<td>720 ± 81(ab)</td>
</tr>
<tr>
<td>Scrub</td>
<td>263 ± 66(b)</td>
<td>218 ± 66(a)</td>
<td>288 ± 66(b)</td>
</tr>
<tr>
<td>Woodland</td>
<td>401 ± 49(ab)</td>
<td>356 ± 57(ab)</td>
<td>146 ± 53(bc)</td>
</tr>
<tr>
<td>Crude protein</td>
<td>45 ± 10(b)</td>
<td>53 ± 10(bc)</td>
<td>85 ± 10(a)</td>
</tr>
<tr>
<td>Moist grassland</td>
<td>10 ± 9(bc)</td>
<td>44 ± 9(ab)</td>
<td>58 ± 9(b)</td>
</tr>
<tr>
<td>Rush wetland</td>
<td>34 ± 10(b)</td>
<td>77 ± 8(a)</td>
<td>88 ± 8(b)</td>
</tr>
<tr>
<td>Coloumgoristis</td>
<td>54 ± 7(b)</td>
<td>62 ± 7(ab)</td>
<td>76 ± 7(ab)</td>
</tr>
<tr>
<td>Scrub</td>
<td>32 ± 8(bc)</td>
<td>25 ± 8(b)</td>
<td>81 ± 8(bc)</td>
</tr>
<tr>
<td>Woodland</td>
<td>56 ± 7(b)</td>
<td>45 ± 8(bc)</td>
<td>22 ± 7(bc)</td>
</tr>
</tbody>
</table>

Different superscripts in one row indicate significant differences (\(P < 0.05\)) between seasons.
Table 4

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Dimension</th>
</tr>
</thead>
<tbody>
<tr>
<td>Harvest coefficient</td>
<td>50 %</td>
<td></td>
</tr>
<tr>
<td>Animal requirement for forage bulk (cattle)</td>
<td>8.09 kg DM AU−1 day−1</td>
<td></td>
</tr>
<tr>
<td>Animal requirement for forage bulk (pony)</td>
<td>4.1 kg DM AU−1 day−1</td>
<td></td>
</tr>
<tr>
<td>Animal requirement for crude protein (cattle)</td>
<td>0.863 kg CP AU−1 day−1</td>
<td></td>
</tr>
<tr>
<td>Animal requirement for crude protein (pony)</td>
<td>0.377 kg CP AU−1 day−1</td>
<td></td>
</tr>
<tr>
<td>Animal requirement for digestible energy (cattle)</td>
<td>23.88 Mcal AU−1 day−1</td>
<td></td>
</tr>
<tr>
<td>Animal requirement for digestible energy (pony)</td>
<td>9.44 Mcal AU−1 day−1</td>
<td></td>
</tr>
</tbody>
</table>

3.1. Case study results

In the case study, grazing capacity was calculated using digestible energy, crude protein, palatability and forage yield characteristics of the available forage on the one hand (Table 3) and the requirements of Highland cattle and Shetland ponies for these forage features on the other (Table 4). Additional adjustments of the requirements of Highland cattle and Shetland ponies for these characteristics of the available forage on the one hand (Table 3) and digestible energy, crude protein, palatability and forage yield character-

3.2. Model evaluation through a sensitivity analysis

In order to distinguish the relative impact of each parameter on the model outcome, a sensitivity analysis was conducted. Data used in the GC estimation in the case study (Tables 3 and 4) were used as reference values in the sensitivity analysis. In order to remain a straightforward picture in the simulations, sensitivity analyses were based on data gathered in only one season and habitat, since habitat type nor seasonality significantly influenced the sensitivity of the model for changes in any of the model parameters. Due to the maximum GC values and high variability between the GC determining factors that were found in autumn 2005 in the case study (Fig. 2), data from this season were selected to run the sensitivity analyses in the species-poor Calamagrostis habitat. GC was simulated using cattle as grazer species and DE as forage quality determinant. Subsequently, the impact of each parameter on the final model output was studied by changing the reference value while the other parameters were kept constant. For each parameter 20 simulations were run. The correcting factors, scrub hide percentage (2029), slope steepness, water supply distance, palatability index and harvest coefficient, were studied within their maximum range. The range's outer values for animal unit requirement are set to a 75% deviation of the reference values. The used protocol and parameter range are listed in Table 5.

The parameters correcting for habitat accessibility (Table 5) protocol simulation series 1 and Fig. 3a–c) show a polynomial rela-

Table 5

<table>
<thead>
<tr>
<th>Series</th>
<th>Subroutine Parameter</th>
<th>Parameter</th>
<th>Range</th>
<th>Reference value</th>
<th>Dimension</th>
<th>Assumption</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Accessibility</td>
<td>Scrub cover</td>
<td>0–70</td>
<td>22.00 %</td>
<td></td>
<td>Other parameters constant</td>
<td>Fig. 3a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Slope steepness</td>
<td>0–60</td>
<td>12.44 %</td>
<td></td>
<td>Other parameters constant</td>
<td>Fig. 3b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Water supply distance</td>
<td>0–3.2</td>
<td>0.8 km</td>
<td></td>
<td>Other parameters constant</td>
<td>Fig. 3c</td>
</tr>
<tr>
<td>2</td>
<td>Forage yield</td>
<td>Accessible and available FY</td>
<td>0–3000</td>
<td>172.4</td>
<td>kg DM ha−1</td>
<td>Other parameters constant</td>
<td>Fig. 3d</td>
</tr>
<tr>
<td></td>
<td>Forage quality</td>
<td>Accessible and available DE</td>
<td>0–5000</td>
<td>3125</td>
<td>Mcal ha−1</td>
<td>Other parameters constant</td>
<td>Fig. 3e</td>
</tr>
<tr>
<td>3</td>
<td>Palatability</td>
<td>PI per species</td>
<td>0–100</td>
<td>0.75 %</td>
<td></td>
<td>Other parameters constant</td>
<td>Fig. 3f</td>
</tr>
<tr>
<td></td>
<td>Harvest coefficient</td>
<td>HC per habitat</td>
<td>0–100</td>
<td>50 %</td>
<td></td>
<td>Other parameters constant</td>
<td>Fig. 4a</td>
</tr>
<tr>
<td>4</td>
<td>Palatability</td>
<td>PI per species</td>
<td>0–100</td>
<td>0.75 %</td>
<td></td>
<td>HC = 100%; other parameters constant</td>
<td>Fig. 4b</td>
</tr>
<tr>
<td></td>
<td>Harvest coefficient</td>
<td>HC per habitat</td>
<td>0–100</td>
<td>50 %</td>
<td></td>
<td>PI = 100%; other parameters constant</td>
<td>Fig. 4c</td>
</tr>
<tr>
<td>5</td>
<td>AU requirement</td>
<td>AU requirement for DE</td>
<td>5.97–41.79</td>
<td>23.88 Mcal AU−1 day−1</td>
<td></td>
<td>Other parameters constant</td>
<td>Fig. 4d</td>
</tr>
</tbody>
</table>

Table 4

Scrub cover, slope steepness, water distance and harvest coefficient; and animal unit requirements for forage bulk, crude protein and digestible energy.

All aboveground living and dead material within each plot was clipped at ground level. Living parts were separated from dead material at species level. Plant samples were dried at 65 °C during a 48-h period. Afterwards, the samples were weighed and milled through a 0.8 mm screen. Forage quality parameters of each species were determined using near infrared spectroscopy (NIRS) for crude protein (CP%) and acid detergent fibre (ADF%). Digestible energy (DE) was calculated using Eq. (12) (Table 1).

Palatability of plants was derived from animal observation sessions at the study site (continuous focal animal sampling according to Altmann (1974), recording diet at plant species level of one focal animal (Lamoot et al., 2005). Diet preference and palatability of each species in the study area were calculated using Eqs. (3) and (4) (Table 1).

Values for the harvest coefficient per habitat type and the nutritional demand per grazer species were based on literature (Dietz, 1989; Lamman, 1994; NRC, 1981a,b, 1985, 1989, 2000a,b, 2001).

In the case study, grazing capacity was calculated using Eqs. (3) and (4) (Table 1).

Finally, grazing capacity was calculated using Eqs. (1)–(12) (Table 1 and Fig. 1).
Fig. 2. Grazing capacity (GC) in consecutive years (2004–2005) and seasons (sp = spring; su = summer; au = autumn; wi = winter) for (a) ponies and (b) cattle, using forage yield (FY), crude protein (CP) and digestible energy (DE) as parameters. GC is expressed in animal units per surface area (AU ha\(^{-1}\)). Error flags indicate maximum GC values based on 1 standard deviation of the forage quantity and quality input features. (c) Cumulative grazing capacity of the study area with cattle and ponies (based on digestible energy as a forage determinant). Negative values indicate undergrazing; positive values overgrazing.

The relationship with grazing capacity. Increasing scrub cover and slope steepness correspond with decreasing GC values. On the other hand, increasing water supply distance initially shows a constant GC until the threshold value of 0.8 km is reached. Afterwards GC gradually decreases. As the reference value for water supply distance falls below the threshold value, the GC outcome in the case study corresponds with the maximum GC value for varying water supply distances. The vegetation describing parameters, forage yield and forage quality (Table 5, protocol series 2 and Fig. 3d and e), show a positive linear correlation with GC. The relationship between animal unit requirements (Table 5, protocol simulation series 5) and GC is characterized by a negative power function (Fig. 3f).

The impact of varying plant palatability and harvest coefficient on the outcome of the model shows a higher level of complexity. Both parameters interfere as the lower value of the palatability index or harvest coefficient is selected in the calculation process (Table 1, Eq. (7)). Therefore, both the interaction of the palatability index (PI) and harvest coefficient (HC) (Table 5; protocol series 3) as well as the sole impact of each parameter on the estimated GC are studied (Table 5, protocol series 4). In Fig. 4a, the relation between varying palatability index values and the model outcome is depicted while the reference value for harvest coefficient (HC = 50%; Table 5) is used. As a consequence of this 50% HC, the curve flattens as soon as PI reaches 50% and the reference value of 75% PI falls within this plateau. Similarly, the positive linear curve, found between HC and GC, flattens once HC exceeds PI (Fig. 4b). In Fig. 4c, HC is set at 100% in order to exclude its contribution to the final outcome. In this case, a positive linear correlation is found between diet preference and GC. An identical curve is found between HC and GC in case PI is set at 100% (Fig. 4c). Consequently, maximal GC is found when both HC as well as PI are set to 100%.
Fig. 3. (a–f) Output of the grazing capacity model for the Calamagrostis habitat using variable input values for scrub cover, slope steepness, water supply distance, accessible and available forage yield, digestible energy content of accessible and available forage, and animal unit requirement for digestible energy, respectively. Grazing capacity is based on the digestible energy content of accessible and available forage. Reference lines (dotted lines) indicate field data gathered in the case study.

On the other hand, minimal GC values are found in case either HC or PI is set at 0%.

4. Discussion

By including both habitat directed traits (such as forage quantity and quality) and animal related traits (such as animal nutritional demands), the theoretically sustainable number of animals in an area can be estimated. In order to avoid overgrazing, corrections are included in relation to the accessibility of terrains. Substantial reductions of the total grazable area are incorporated in order to correct for steep slopes, water supply distances and scrub hindrance. By including a harvest coefficient, a certain percentage of the present forage can be allocated to other herbivores such as insects and wildlife (deer, rodents, lagomorphs, ...). In order to preserve habitat health, to prevent soil erosion and to assure sufficient plant regrowth, a certain amount of vegetation should remain intact. In general, a 50% harvest coefficient is recommended for maintenance of rangeland habitats in sustainable condition (Dietz, 1989; Lamman, 1994). However, when nature conservation management is involved, the harvest coefficient of the composing habitats of a nature reserve should be adjusted according to the manager’s needs. Whether they will be realized depends on the combined palatability and harvestability indexes per habitat. Grazing management in nature reserves generally aims at maximization of biodiversity through increased spatial heterogeneity. According to the present situation and the goals to be achieved in the future the harvest coefficient can be set to a higher or lower level. In habitats with low species diversity, such as the rough grassland habitat type, managers should temporally increase grazing densities to push back grass encroachment and to create niches for other plant species (Kooijman and de Haan, 1995). On the other hand, in case of vegetations sensitive to trampling or grazing, the harvest coefficient should be set to a lower level in order to lower the probability of habitat deterioration.
In this paper, grazing capacity is determined using three forage parameters: forage yield, crude protein and digestible energy content of the available, consumable and accessible vegetation. These determinants lead to miscellaneous results in the GC model outcome. All three forage characteristics are highly context dependent and should therefore be established separately for different ecosystems (e.g. Milotic et al., 2008, who compared dune with salt marsh conditions). For the case study area, it appears that digestible energy is generally the most restrictive parameter, while crude protein was generally least restrictive. This suggests that in this particular case, GC estimates should rather be based on (digestible) energy than on forage yield. However, in most of the traditional methods used in rangeland conditions the latter is generally used (e.g. Holechek, 1988; Kothmann and Hinnant, 1992; Steenekamp and Bosch, 1995). Only in one season during the two-year study period, forage yield appeared to be the most limiting factor, i.e. in spring 2005 when forage yield was very low and protein content and digestible energy per unit plant weight of newly outgrowing shoots was high.

With the actual management strategy of the area, grazer density exceeds optimum grazing capacity in winter and spring 2005, while grazing pressure is (too) low in summer and autumn. Nevertheless, this pattern is less explicit in 2004, when smaller amounts of digestible energy were available in the area. Compared to 2005, precipitation was low in 2004 which led to lower forage yield and thus available digestible energy in that year (Ebrahimi, 2007). This practice involves a risk of overgrazing in winter and spring, and undergrazing in the other seasons, resulting in the harvest of more respectively less than 50% of the present herbage. In the current situation, the management objective of a 50% HC is only accomplished in a part of 2004, which implies that the year-round grazing management with a constant herd composition and density should be reconsidered.

As phytomass production and forage quality in temperate grasslands both strongly depend on weather conditions (e.g. radiation, mean daily temperature, precipitation, evapotranspiration) and site characteristics (e.g. nitrogen availability, soil water-holding capacity) (Jouven et al., 2006a,b), grazing capacity cannot be considered as a static feature within and between years and throughout ecosystems. Furthermore, as variations in phytomass production are to be expected between consecutive years, GC should be considered as a dynamic feature. Hence, a discrimination between short-term and long-term GC appears necessary. So far, grazing capacity in rangeland management is mostly considered as a static factor and short-term GC estimates are often extrapolated to other seasons and years (e.g. de Leeuw and Tothill, 1993), often resulting in misleading long-term GC estimates (Vallentine, 2001). Also in nature conservation management so far, little attention is given to temporal differences in grazing capacity, although recently the idea of grazing time gaps (e.g. Van Uytvanck et al., 2008) or introduction of seasonal fluctuations in grazer densities (Hester et al., 1996), is gaining interest.

In the sensitivity analysis, all used input parameters correlate strongly with the model output and have a significant impact on model outcomes. Apart from forage yield and digestible energy, no linear correlations are found between the model input and output. Moreover, each input factor has a different trend line, which implies that simplification of the model not only depends on the maximum sensitivity of a factor, but also on the sensitivity of the range of the variable. In case an input variable is situated in the sensitive part of its range, elimination of this factor would result in an inconsistent GC estimate. In the case study, the factor correcting for water sup-

![Fig. 4. (a–c) Output of the grazing capacity model for the Calamagrostis habitat using variable input values for plant palatability and harvest coefficient. (a and b) Represent the model output in case all other parameter values are kept constant; (c) represents the model output in case the parameter values for harvest coefficient and palatability are set to 100%. Grazing capacity is calculated using the digestible energy content of accessible and available forage. Reference lines (dotted lines) indicate the case study’s input values.](image-url)
ply distance can be eliminated as the input variable is situated in an insensitive part of the parameter range. Alternatively, the elimination of the factor correcting for scrub hindrance in the case study would lead to an overestimation of GC.

Therefore, it appears that none of these factors can be eliminated from the model without significantly altering the model outcomes. Simplification of the model structure would lead to greater uncertainties about the accuracy of the GC estimation. Another point of interest and concern is the combined effect of the harvest coefficient and palatability index on the model outcome. As in the calculation of the available and accessible amount of forage yield the lower value of both indices is used, caution is recommended in case of extreme values. Supposing the harvest coefficient is rather high and the vegetation is unpalatable, low grazing capacity will be predicted while temporally high grazing pressure could be advisable in order to suppress competitor dominated vegetation. On the other hand, in case the vegetation is vulnerable but palatable, low grazing capacity is predicted by the model (due to the low harvest coefficient), while one might expect that grazers will select this palatable vegetation particularly.

Therefore, we advise managers to use the model with additional care in case vulnerable, palatable vegetation units are present in the grazing block – which would require low grazing densities or exclusion from the grazing area – or when grazing management is applied in order to push back grass or scrub encroachment, which would require temporally increased grazer densities. In any case, good knowledge of the ecosystem (species diversity, temporal variations in forage yield and quality, ...) and a clear definition of the aims of the grazing management (e.g. conservation of species diversity or restoration of vegetation types) will lead to successful landscape management.

5. Conclusions

Returning to the research questions raised, we can state that (1) we managed to develop a grazing capacity model that takes into account all parameters that significantly impact grazing capacity, enabling fine-tuning of sustainable nature conservation as well as rangeland management, and that the number of determinants cannot easily be reduced. We further conclude that terrains as well as animal characteristics are relevant in optimizing grazing capacity estimation, and that the model is sensitive to changes in any of the determinant estimates; (2) grazing capacity is a dynamic feature, due to seasonal and even between years fluctuations in forage quality and quantity, which hence needs to be considered when aiming at an accurate grazing capacity estimation; and (3) digestible energy may limit grazing capacity more strongly than forage yield or crude protein, at least in a coastal dune area such as studied in the case study. We therefore suggest the use of (digestible) energy, rather than protein or forage yield, as a measurement factor of forage, since the most conservative grazing capacity estimates were given, using this measure.

As far as the case study system is concerned, we can state that due to fluctuations in herbage availability and quality within and between years, seasonal alterations in optimal grazer densities occur. Year-round grazing with a constant herd size involves a risk of overgrazing in summer and autumn and undergrazing in the other seasons. This underpins the strategy in nature as well as rangeland management to have fluctuating herd sizes in function of available and accessible forage characteristics and animal needs.

Notwithstanding the application of the GCM in a coastal dune environment, the model is applicable in other situations provided that site-specific input data are available. As the model output is highly influenced by the combination of the harvestable portion of phytomass (from the manager’s perspective) and the palatability of forage (from the grazer’s perspective), correct estimation of these parameters is indispensable for an accurate GC calculation.

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References


