Space use, herbage selection, and animal performance of grazing heifers on a peaty river valley section

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ABSTRACT
Grazing is a suitable option for managing the habitat functions of restored fen grasslands. Nevertheless, nutritional requirements of the grazing livestock need to be considered to make such grazing systems sustainable. In order to analyze the interactions between the development of forage nutritive values, grazing behaviour and resulting liveweight gains, we implemented a grazing experiment at a typical river valley section in Northeast-Germany. We tested the hypothesis that heifers were able to compensate the decreasing digestibility of pasture growth over the course of the grazing period by selective grazing. Herbage on offer and faeces of heifers were sampled and analyzed biweekly from May to October over three grazing seasons. The nitrogen content of the faeces was used to estimate the digestibility of the selected herbage. The sedge-dominated peat area was not used for grazing before the grass-dominated sections of the moraine area were depleted, despite acceptable energy contents of the sedge-dominated plant communities during spring and early summer. This behaviour limited the degree of energy selection. The energy content of the herbage on offer explained 67% of the variations in daily liveweight gain. Results indicate the need to modify the management of continuous stocking systems for achieving economically feasible gains.

1. Introduction
The sparsely populated landscape of north-eastern Germany is characterized by elongated glacial river valleys at the bottom of which percolation mires have formed (Janke 2002). While the slopes of these valleys consist of mineral sediments of the glacial moraines, the central parts are structured by deep peat bodies fed by groundwater (Michaelis and Joosten 2002). These peat bodies represent large carbon reservoirs, ensure good water quality through their filter function and also serve as important water reservoirs at the landscape scale (Joosten and Succow 2001). Since the 1960s, agricultural use in this part of Germany has intensified in the form of increasing arable use of the mineral flanks and melioration of the central peat sections for silage-based forage production resulting in a loss of the attendant regulating ecosystem functions. Since the socio-economic upheavals of the 1990s, this type of land use has been largely replaced by extensive grazing systems (Müller and Heilmann 2011). However, at some valley sites land use was completely abandoned (Koch and Jurasinski 2015). Today, efforts to enhance the ecological value of these landscape sections were intensified with the objectives of soil protection (Negassa et al. 2019), reduction of greenhouse gas emissions (Sachs et al. 2016), increase in biodiversity (Fischer 1999; Middleton et al. 2006) and improvement of water quality (Mander et al. 1995). The role of large-scale, low-density grazing to achieve these ambitious goals in river valleys with degraded fen cores was investigated by Schrautzer et al. (2016). The authors confirm the general suitability of large-scale cattle grazing as a tool for biodiversity restoration but yielded ambiguous results concerning achievement of restoration goals in detail. The structure-and thus also biodiversity-promoting effect of extensive grazing is mainly based on the selective feeding behaviour of cattle (Adler et al. 2001) and has in addition to a temporal (Evans et al. 2004) a spatial dimension (Schaich et al. 2010). Since the latter one varies strongly (Pickert and Müller 2016), especially in geomorphological heterogeneous sceneries (Gersie et al. 2019), further scale- and site-dependent studies are necessary to unravelling the partly contradictory results of large-scale grazing implementation on different regulating ecosystem services.

But even if the potentials and risks of large-scale grazing systems for a special landscape type are largely known, e.g. as in the studies of Luoto et al. (2003), the combination of regulating ecosystem services with economically sustainable meat production as a provisioning service remains a major challenge, especially at river valley sites (Hornung et al. 2019). At a regional landscape scale, appropriate grazing practices have to be developed to meet the challenges of maintaining the natural resources while establishing socio-economically sustainable land use systems (Ostermann 1998; Birge and Herzon 2014). Low-density grazing in semi-natural areas with restricted nutritive value of the dominating plants requires high individual animal gains to be economically viable (Orr et al. 2019).
Under continuous stocking, the ability of the single animal to graze selectively is the most important adaptation mechanism to meet nutritional demands (Weissbach 1993). It is known that forage selection of cattle depends on vegetation patterns (Lazo and Soriguer 1993; Mayer et al. 2003; Hessle et al. 2008), and sward structure (Griffiths et al. 2003; Mezzalira et al. 2014). However, only a few studies have related forage selection criterion to seasonal development of liveweight gain against a defined semi-natural backdrop (Strodthoff 2003; Mitsch 2009).

Furthermore, pasture size in forage selection experiments is often restricted to <1 ha or even to a plot size dimension. Under such small-scale conditions, realized selection can be regarded as a choice decision by the animal without the necessity of weighing up the energy input required (‘selection costs’). Under geomorphological heterogeneous rangeland conditions, two further factors supervene: the length of distances to realize theoretical selection potential and the increasing stratification in forage nutritive value. Both spatial vegetation conditions may limit the selection amplitude in the practice of semi-natural grazing (Ganskopp and Bohnert 2006). Thus, the mechanisms governing grazing selectivity and in turn the factors controlling live-weight gain on large pasture units on typical river valley sites are not fully understood.

This study aimed to analyze the dynamics of forage value development during the grazing season, the corresponding degree of grazing selectivity and related animal performance of cattle under free access conditions during the complete grazing period in the presence of strong contrasting plant communities that typically occur at peaty river valley sections. We addressed the following questions:

(i) Are heifers able to compensate the expected decreasing digestibility of pasture growth over the course of the grazing period by selective grazing?

(ii) Are the possibilities for grazing heifers to improve their diet by selective grazing limited by disproportional development of forage values of contrasting plant communities widely spaced over a large-scaled grazing area?

(iii) Can variations in daily liveweight gain be largely explained by levels of the metabolizable energy content of the diet during the grazing season?

2. Materials and methods

2.1. General experimental approach

The grazing experiment was conducted on a typical river valley segment consisting of a percolation mire and an adjacent moraine slope (see Figure 1, Peene valley, northeast Germany, 51°88’N, 13°00’E). This segment with a size of 13 ha was used as a set stocking pasture over three grazing periods. Continuously stocked heifers had free access to the complete area. Stocking densities were 1.01, 1.24 and 2.0 livestock units (LU) per ha for the grazing seasons 2011, 2012, and 2013, respectively (see Table 1). Development of animal related traits were continuously recorded on the individual level and linked to biweekly collected data of sward characteristics. The spatial usage pattern of the herd was indicated by the height

| Experimental year | Number of animals | Livestock units (LU) | Stocking density (LU ha⁻¹) |
|-------------------|-------------------|----------------------|---------------------------|
| 2011              | 22                | 13.2                 | 1.01                      |
| 2012              | 27                | 16.2                 | 1.24                      |
| 2013              | 27                | 16.2                 | 1.24                      |

One heifer corresponds to 0.6 livestock units (LU).

2.2. Study site

The low-lying peat area (WRB: Folic Histosol) covered 60% of the grazing area. The other part of the pasture was a slope of calcareous loamy sand (WRB: Luvisol) increasing to a height of 9 m above the river level over a distance of 170 m.

Climatic conditions during the three experimental years varied markedly (see Supplementary Figure S1). The groundwater level of the undrained peat area was near the surface for some periods of the grazing seasons (see Supplementary Figure S2), whereas the moraine area was completely rain-fed. The high precipitation rates in the summer of 2011 led to a flooding event. The inundation lasted for three weeks and prevented the cattle from grazing on the peat area for the rest of the grazing season.

Plant available soil nutrient contents at 0–10 cm soil depth in the moraine area were 3.1 mg 100 g⁻¹ PDL on average (standard deviation (sd) 1.8), 14.8 mg 100 g⁻¹ KDL (sd 6.7), and a pH-value of 5.03 (sd 0.42) was measured. In the peat area, soil contents of 2.8 mg 100 ml⁻¹ PDL on average (sd 1.4), 30.7 mg 100 ml⁻¹ KDL (sd 13.0) and a pH-value of 6.66 (sd 0.36) could be found, respectively.

2.3. Vegetation and management history

The semi-natural pasture has neither been reseeded nor been fertilized for at least 25 years. The vegetation has mainly
been determined by a moisture gradient from the top of the slope to the lower parts near the river and can be classified in eight main associations according to Berg et al. (2004). At the moraine area, the main association was *Lolium perenne* – *Cynosuretum cristati* (Tx. 1937) with *Agrostis capillaris*, *Festuca rubra*, *Holcus lanatus* and *Cynosurus cristatus* as dominant species. The peat area showed a greater phytodiversity characterized by grazed flood plain plant communities like *Ranunculo repens* – *Alopecuretum geniculata* (Tx. 1937) and wet meadow associations like *Cirsi oleracei* – *Angelicitetum sylvensis* (Tx. 1937). A high share of the peat area hosted sedges (*Carex nigra*, *C. rubra* for a sporadic cleansing cut at the end of the grazing season. Like fertilization, drainage or reseeding were applied except (LU) per ha. No common grassland improvement measures managed in the last 25 years as a continuously stocked pasture with a stocking rate of less than 1.3 livestock units (LU) per ha. No common grassland improvement measures like fertilization, drainage or reseeding were applied except for a sporadic cleansing cut at the end of the grazing season.

### 2.4. Grazing management

The cattle were crossbreed beef cattle (*Simmentaler × Limousin × Charolais*), weaned at the end of the previous grazing season at a mean weight of 320 kg. Grazing intensities are shown in Table 1.

The slightly increased stocking rates in 2012 and 2013 compared to 2011 (Table 1) were due to the recommendation of the nature conservation authority. The aim was to reduce the competition of the sward somewhat in order to promote the valuable orchids (mainly *Dactylorhiza majalis*). In 2011, the animals were brought to the pasture on the 4th of May. In midsummer 2011, a flooding event prevented access to the peat area for the remaining time of the grazing season. Due to the reduced forage availability, grazing ceased on September 17th in 2011. Because of the relatively high temperatures in spring 2012 (Figure S1), the growth of grass started early. Thus, the animals were stocked on the pasture already on the 23rd of April. As a consequence of the even distribution of precipitation, grazing continued until the 23rd of October in 2012. The winter 2012/2013 was strong and the temperature remained under 0°C until the second week of March (see Figure S1). Therefore, the start of the grazing season was delayed until May 16th in 2013. Due to the decreasing forage availability in early autumn, grazing ceased on the 30th of September in 2013.

### 2.5. Animal related measurements

All animals were equipped with electronic earmarks (Allflex®,) allowing for identification at an automatic weighing system (TruTest3000®). The animals were attracted to the weighing system by a bucket of mineral supplementary feeding. Data was used to calculate the daily liveweight gain (DLG) for the biweekly periods between two herbage and faeces sampling events.

At each herbage sampling event, six samples consisting of six subsamples of fresh cattle faeces were collected to analyze the nitrogen content after drying to a constant weight at 65°C and grinding to 1 mm. N content of faeces (FaecN) was measured using dry combustion technique (CNS analyzer varioMAX®). FaecN enables the estimation of the digestibility of the selected diet according to Schmidt et al. (1999)

\[
\text{DOM diet} = \frac{95.90 - \left( \frac{460}{\text{FaecN}} \right) - 0.1582 \times \text{GDN} + 0.00062 \times \text{GDN}^2}{100}
\]

where FaecN is the N content (g kg⁻¹; standard error of prediction not given) of faecal organic matter (excluding ash) and GDN is the number of grazing days counted from 30 April onwards.

The representativeness of the leading animals for the herd position was confirmed several times by binocular observations in 2011 and 2012. Only towards the end of the grazing period, when there was a lack of attractive herbage on offer, did the herd association disintegrated. The results of these observations revealed that not one, but up to three high-ranking heifers made the spatial relevant decisions. In the last experimental season 2013, the opportunity arose to replace the random observations of the two previous years by equipping a lead animal with a GPS collar. Therefore, we specifically implemented a slightly older and not dehorned heifer in the herd which, as hoped, showed a clear dominant rank. Animal positions of this leading animal (see Figure S3 in the Supplements) were recorded every 5th minute using a collar with GPS receiver (Vectronic Aerospace GmbH, Berlin, Germany) in 2013. The precision of the GPS receiver was <2.9 m from the true position for > 90% of the data.

### 2.6. Forage related measurements

Herbage was sampled along transect lines following the moisture gradient from the top of the sandy slope down to the lower parts adjacent to the river (see Figure 1). Ten of the sampling points were situated on sandy soil (moraine area), while 14 of them were situated on peat soil (peat area). This transect represented the typical soil – vegetation constellation, which could be found on the whole pasture.

#### 2.6.1. Determination of the herbage mass on offer

To record the development of herbage mass over the grazing seasons, the sward was sampled biweekly from May to October at the 24 transect points. The sampling scheme applied for each of the transect points is shown in the Supplementary Figure S4. The sward height was measured six fold using a 30 cm × 30 cm square rising-plate meter (Herbometre®, France) at randomly chosen positions in a radius of 3 m around each sampling point. From these sward height measurement-points four herbage samples were taken by cutting the material, within the 30 cm × 30 cm squares measured before, to 4 cm above the ground using a lawn shears (see Supplementary Figure S5). Only where the
vegetation had been grazed deep, samples were cut to 1 cm above the ground to reproduce the actual grazing intensity of the vegetation points. These four herbage subsamples were thoroughly mixed.

2.6.2. Determination of the forage quality parameters of the pasture growths

The herbage samples were then dried in an air circulating drying oven (Horo®, Ostfildern, Germany) at 45°C to a constant weight. This took between 24 and 36 h, depending on sample characteristics. Dried samples were ground to 1 mm mesh size using a rotary mill (Brabender®, Duisburg, Germany) afterwards. For analyzing the nutritive value parameters crude protein (CP), crude fibre (CF), neutral detergent fibre (NDF), acid detergent fibre (ADF), and enzyme insoluble organic matter (EULOS), near infrared reflectance spectroscopy (NIRS, MPA Bruker®, Ettlingen, Germany, VDLUFA fresh grass calibration fg2011; SEP = 2.4%) was used. In accordance with the reference standard methods (Naumann and Basler 2012), crude ash content and a sample subset selected by spectral information were standard methods (Naumann and Basler 2012), crude ash content and a sample subset selected by spectral information were additionally analyzed chemically to fit the NIRS calibrations to the experimental data set.

Based on these primary quality parameters, digestibility of the offered herbage (DOM offer) and metabolizable energy (ME) were calculated according to Weißbach et al. (1999):

\[
\text{DOM offer} = \frac{100 \times (940 - XA) - (0.62 \times \text{EULOS}) - (0.00022 \times \text{EULOS}^2)}{(1000 - XA)}
\]

where DOM offer is the digestibility of the organic matter (%) DM; SEP = 3.8%, EULOS is the enzyme-insoluble organic substance (g kg\(^{-1}\) DM) and XA is the crude ash content (g kg\(^{-1}\) DM) as determined by heating samples in a muffle furnace.

\[
\text{ME} = 13.98 - (0.0147 \times XA) - (0.0102 \times \text{EULOS}) - (0.00000254 \times \text{EULOS}^2) + (0.000234 \times XP)
\]

where ME is the metabolizable energy (MJ ME kg\(^{-1}\) DM; SEP = 3.7%), EULOS is the enzyme-insoluble organic substance (g kg\(^{-1}\) DM), XA is the crude ash content (g kg\(^{-1}\) DM), and XP the crude protein content (g kg\(^{-1}\) DM).

2.7. Data analysis

Differences in forage quality traits between soil types and time of season were analyzed by ANOVA followed by post hoc tests (Tukey HSD) using the R 3.3.2 software environment (R development Core Team 2016). In case of CF and ME, where the observations were not normally distributed (verified using the Shapiro–Wilk-Test) and had different variances, a linear mixed model (LMM) approach was applied. We used the R package ‘lme4‘ (Bates et al. 2015) to run LMM.

Multiple linear regression (MLR) was chosen to model Daily Liveweight Gain (DLG) for explaining variables by different approaches: In a first approach, DLG related forage quality and availability parameters of all three experimental years, separated according to the soil type, were referred to. In addition, the data for the 2013 grazing season were modelled separately, as they also allowed the inclusion of the residence data. In both approaches a complete model was first calculated using the ‘MASS’ package (Venables and Ripley 2007). In a second step, a stepwise regression fit according to the Akaike information criterion (AIC) was applied. The statistical model parameters of the full and the stepwise reduced models were tabulated comparatively.

In addition to these exploratory analyses, the correlation between the energy content of the pasture growth and the liveweight gain was quantified by linear regression. Due to the restricted forage availability caused by the flooding event in 2011, three values were excluded from this calculation. In order to present a realistic relationship between both variables, only the energy content of sampling points in areas that were really used by the animals were considered.

The forage selection success was graphically presented as the distance between the digestibility of offered and ingested forage using statistic and graphic tools of SigmaPlot 14.0®.

The GPS collar was removed after the end of the grazing season 2013. GPS data was downloaded and merged with pasture area data using the GIS software ArcMap® (ESRI, 2002). The distribution of the animals within the area was analyzed using a kernel density approach. The kernel density was computed with an 18 m search radius at 3 m grid size, using ArcGIS® 10.5 (ESRI, 2017).

3. Results

3.1. Seasonal trends in herbage mass development

Overall, the patterns in herbage mass development during the grazing seasons were similar for the years we researched, although there were significant differences (\(P < 0.001\)) between the peat and moraine areas (Figure 2).

In the moraine area, the height decreased to a minimum that was reached approximately in the middle of the grazing season and remained constant until the end. A taller sward was found in the peat area from the outset. The sward height in the peat area did not decrease until the minimum sward height in the moraine area was reached (Figure 2).

3.2. Seasonal trends in herbage quality development

In each year, the content of CP decreased in the moraine area until the 11th week after the 1st of May, followed by a slight increase (Figure 3). In contrast, CP decreased in the peat area during the whole grazing season, except in the year with a summer flooding event (2011). Overall, the content of CF was higher in the peat area compared to the moraine (\(P < 0.05\)) and tended to increase during the grazing season. The range for CP and CF variations was larger in each year in the moraine area, which is indicated by the error bars (Figure 3).

Overall, the content of ADF was found to be lower in the moraine area (\(P < 0.05\)). This also applied for NDF, except for 2012, where a high level of NDF generally occurred. The energy content was always higher in the moraine area in each of the experimental years (Table 2).
Figure 2. Seasonal development of mean sward height as a proxy of herbage mass on offer in the moraine (closed circles) and peat area (open circles). Interruption of measurements 2011 in the peaty part of the pasture due to a heavy summer flooding event.
Figure 3. Development of crude fibre CF (% DM) and crude protein CP (% DM) in the grazing seasons 2011, 2012 and 2013 on the moraine and on the peat part within the freely accessible total pasture area.
Shown are estimated means and their standard errors of all measurements over the grazing season of July. As the grazing period progresses, the difference in animal feeding preferences between the two soil types become blurred. Furthermore, it can be seen from the decreasing colour intensity that the overall moving activity decreases towards the end of grazing in autumn (see also Figure S6 in the supplement).

### 3.3. Seasonal pattern of spatial land use

As can be seen in Figure 4, the preference of grazing animals to stay on one or the other soil type shows a seasonal pattern. During the first four weeks, the cattle stayed almost exclusively on the moraine grassland; they made only sporadic visits to the peat site. The heifers only start to make greater use of the peat areas from the 7th week after the 1st of May, at a time when the growth of the moraine area had ceased (see Figure 2, year 2013, week 7). The same residence density as that on the moraine area is reached on the peat area from the beginning of July. As the grazing period progresses, the differences in animal feeding preferences between the two soil types become blurred. Furthermore, it can be seen from the decreasing colour intensity that the overall moving activity decreases towards the end of grazing in autumn (see also Figure S6 in the supplement).

### 3.4. Animal performance

The main characteristics of animal performance such as the herd average of liveweight gain per grazing season and the resulting daily liveweight gains are presented in Table 3.

The highest individual animal performance was achieved in the 2011 grazing period with an average daily liveweight gain of 828 g per head. The longest grazing season (2012) resulted in significantly lower grazing performance of 600 g liveweight gain per heifer and day on average. In 2013, the year with the highest grazing start weights, only 420 g liveweight gain per heifer and day on average. In 2013, the year with the highest grazing start weights, only 420 g liveweight gain per head. The longest grazing season (2012) resulted in the moraine area on a comparable level with a decreasing trend (Figure 6). At this stage, the estimated digestibility of the selected diet (DOMdiet) was found to be on this level too.

From the 11th week after the 1st of May the DOMoffer in the moraine and the peat area changed inversely: while it increased in the moraine area, it decreased in the peat area. The DOMdiet could be found to be slightly lower than the DOMoffer in the moraine area from this point onwards, whereas the DOMoffer in the peat area dropped. In 2013 the DOMoffer in the peat area was 15% lower from the beginning of the grazing season compared to the DOMoffer of the moraine area, with a faster decline from the 10th week after the 1st of May.

### 3.5. Extent of selection for digestibility

At the beginning of the grazing season in 2011 and 2012, the digestibility of organic matter of the herbage on offer (DOMoffer) in the moraine and the peat area was on a comparable level with a decreasing trend (Figure 6). At this stage, the estimated digestibility of the selected diet (DOMdiet) was found to be on this level too.

### 3.6. Variables affecting daily liveweight gain

Multiple linear regression analysis was applied to develop a model for depicting daily liveweight gain (DLG) from the variables related to forage value and availability. While the compressed sward height (CSH) can be regarded as a proxy for forage availability, the other variables included in the complete model relate to parameters of forage value, divided between the two soil types. When selecting the characteristics of the forage value, importance was attached to the lowest possible intercorrelation. As digestibility of organic matter (DOM) and metabolizable energy content (ME) are closely correlated and DOM is a primarily measured and not derived characteristic, it was included in the model. The more complex characteristic ME with its strong intercorrelations to XA, XP and DOM was subjected to a separate consideration.

The results of the MLR analysis are presented in Table 4. The parameters CSH on the moraine part and the digestibility of the growths on the peat part had the greatest significance to explain DLG. Estimates derived from all other variables proved to be not significant.

The data for the 2013 grazing season, which included the residence densities, were modelled separately in the same way. The results are shown as Table S2 in the supplement. Only the reduced model could be used for DLG-explanation, and this is based only on the parameters of residence densities. For this reason, the relationship between the residence density

### Table 2. Acid detergent fibre (ADF, % DM), neutral detergent fibre (NDF, % DM) and energy content (ME, MJ kg \(^{-1}\) DM) for the grazing seasons 2011, 2012 and 2013 in the moraine and peat area.

| Season | Moraine | Peat |
|--------|---------|------|
| 2011   | 31.96 (0.27) | 36.21 (0.34) |
| 2012   | 35.35 (0.27) | 37.84 (0.23) |
| 2013   | 32.03 (0.26) | 37.15 (0.22) |

| Season | Moraine | Peat |
|--------|---------|------|
| 2011   | 50.93 (0.41) | 55.00 (0.51) |
| 2012   | 58.89 (0.40) | 58.45 (0.34) |
| 2013   | 53.41 (0.39) | 57.01 (0.33) |

| Season | Moraine | Peat |
|--------|---------|------|
| 2011   | 10.37 (0.06) | 9.06 (0.07) |
| 2012   | 9.78 (0.06) | 9.15 (0.05) |
| 2013   | 10.16 (0.06) | 8.51 (0.05) |

**Table 2**. Grazing period (d)

| Season | Moraine | Peat |
|--------|---------|------|
| 2011   | 288.96 (16.23) | 401.60 (8.45) |
| 2012   | 267.90 (17.64) | 377.78 (28.36) |
| 2013   | 369.79 (20.20) | 427.25 (17.80) |

**Table 3**. Mean weight gain per grazing season and resulting liveweight gains.

| Grazing season | Start of grazing | End of grazing | Mean weight gain (kg) |
|---------------|------------------|----------------|-----------------------|
| 2011          | 288.96 (16.23)   | 401.60 (8.45)  | 112.64                |
| 2012          | 267.90 (17.64)   | 377.78 (28.36) | 109.88                |
| 2013          | 369.79 (20.20)   | 427.25 (17.80) | 57.46                 |

**Table 3**. Mean liveweights of grazing heifers at the start and at the end of the three grazing seasons and resulting liveweight gains.
and the weight increases was additionally illustrated graphically in Annex Figure S6.

DLG (g d$^{-1}$ head$^{-1}$) followed the corresponding energy content (ME MJ kg$^{-1}$ DM$^{-1}$) of the herbage on offer (Figure 7). Overall, nearly 67% of the variation in DLG can be attributed to this metabolizable energy concentration. For the interpretation of the results, it is important to note that this energy content is shown as the average of all considered sampling points.

4. Discussion

4.1. Suitability of extensive cattle grazing for a sustainable management of peaty river valleys

The overall objective of choosing integrated management for river valleys is to optimize ecosystem services in a way that ensures the protection of natural assets while maintaining the sustainable use of resources (Thorpe et al. 2010). In this respect, the use of the river flank areas as arable land is ruled out as an option to meet these goals due to carbon depletion, GHG emissions (Wichtmann et al. 2016), and the risk of erosion and eutrophication (Mander et al. 1995). This means that afforestation and use as grassland remain under consideration.

According to Chrzanowski and Kaca (2001), grassland has advantages over forest in terms of conservation of the groundwater reservoir and soil protection as regulating ecosystem services in peaty river valleys. Kumm and Hessle (2020) compared the economic merits of using land as forest or as grassland for beef production. They concluded that extensive organic cattle farming could be more profitable than forestry, especially, if government subsidies in the form of financial support and environmental payments are available. Apart from the provisioning service of maintaining cattle production, biodiversity (Middleton et al. 2006) as well as aspects of special species protection (Fischer 1999) play an important role as cultural and regulating services in peaty river valleys. For the site investigated here, Müller and Sweers (2016) have already been able to prove that extensive cattle grazing for beef production can maintain and enhance the high potential of the site to host rare plant species. Nevertheless, the compatibility of extensive beef production with the promotion of biodiversity while at the same time conserving soil and water resources remains a major economic challenge. Forage selection of grazing cattle and associated space use are at the core of this challenge for two reasons: on the one hand, because the forage selection success is decisive for the individual animal performance (Breitsameter et al. 2017) and thus for the economic efficiency of
land use, and on the other hand, because the heterogeneity pattern in vegetation created by selective grazing is a prerequisite for a high level of biodiversity (Tonn et al. 2019). Therefore, the following sections deal with the spatial and temporal processes necessary to understand the interaction between herbage selection and the generation of animal performance.

4.2. Sward height development

The pasture in our study was continuously stocked during the grazing season as well. Therefore, a constant distribution of the grazing activity by the heifers would have been expected to lead to the sward height being maintained at a nearly constant height over the whole pasture. Nevertheless, the development of sward height in both areas indicated that heifers tended to be attracted to the moraine area in spring. During this period, grazing events were observed exclusively in the moraine area. A higher preference especially in spring for short pure grass patches has also been reported by Dumont et al. (2007). Due to this behaviour, a slight decrease in the sward height could be found in the moraine area from the 1st till the 9th week after the 1st of May in each year (Figure 2). In 2012 and 2013, a decrease in sward height was observed in the peat area, when the sward height in the moraine area fell below 60 mm due to initial grazing activities of the heifers in the peat plant communities. The decrease in sward height in the peat area from the 6th to the 10th week was not ascribed to grazing, but rather to heavy rainfall events that caused the vegetation to collapse. The decrease in sward height in the peat area after the first of May, that is, in mid-July. This may, in fact, signify the point when the herbage mass on offer in the moraine area was depleted and the heifers had to graze in the peat area instead. As indicated by the sward height in both areas, it was clear that the heifers did not graze the whole pasture evenly during the grazing season.

4.3. Physiological development of pasture growths

The uneven temporal and spatial distribution of the grazing activity during the grazing season can be explained by a closer examination of the physiological development of pasture growth in both the moraine and peat areas. We used CP and CF as indicators of the physiological stage of grasses and herbs since these proxies are also related to the palatability of growths (Heady 1964). While CP started at a similar level at the beginning of the grazing season in our study, CF was higher in the peat area (Figure 3) as a result of the dominating wetland species being morphologically better adapted to high water levels. In a further development, a decrease in CP and an increase in CF could be found in both areas as an expected effect of advancing plant maturity. Although this development reversed by the 11th week after the 1st of May in the moraine area, it continued in the peat area. It can be concluded that the uneven grazing activity in both areas led to a regrowth of phenologically young herbage in the moraine part and to a more mature herbage in the peat area. As a result of these opposing developments, the content of CP in the moraine area increased, while it was CF that increased in the peat area (Figure 3). This effect was also described by Dumont et al. (2007). They conclude that more and less intensively grazed areas of herbage

Figure 5. Trends of daily liveweight gains and losses (DLG, g head⁻¹ d⁻¹) in the course of the grazing seasons. The white dots represent the biweekly calculated DLG herd means, the error bars the standard deviation of the means.
Figure 6. Digestibility of the organic matter of the herbage on offer DOMoffer moraine % and DOMoffer peat % versus digestibility of the realized pasture diet (DOMdiet %) by the heifers at each of the three grazing seasons. Error bars indicate standard deviations of the DOM means.
**Table 4.** Multiple regression modelling of the Daily Liveweight Gain (DLG) related forage quality and availability parameters separated according to the soil type.

| DLG model comparison | Full model | Reduced model |
|----------------------|------------|---------------|
| DOM on offer – moraine | 24.838 (40.210) | 23.658 (22.528) |
| DOM on offer – peat | 21.428* (10.705) | 19.121 (8.930) |
| CSH – moraine | 14.232** (5.851) | 11.477** (4.763) |
| CSH – peat | 2.587 (1.960) | 1.912 (1.303) |
| XP – moraine | 3.585 (4.110) | 2.734 (2.498) |
| XP – peat | 3.655 (3.618) | 2.734 (1.898) |
| NDF – moraine | 3.882 (3.674) | 2.734 (1.898) |
| NDF – peat | –0.102 (3.618) | 2.734 (1.898) |
| Constant | –6,962.255 (5.148.144) | –2,028.422*** (496.555) |
| Observations | 27 | 27 |
| $R^2$ | 0.788 | 0.771 |
| Adjusted $R^2$ | 0.694 | 0.730 |
| Residual Std. Error | 229.213 (df = 18) | 215.487 (df = 22) |
| $F$ Statistic | 8.369*** (df = 8; 18) | 18.530*** (df = 4; 22) |

Note: *P < 0.1; **P < 0.05; ***P < 0.01.

Shown are the model estimates and their corresponding standard errors in brackets.

lead to a reinforcement of spatial heterogeneity. This process reinforced the already existing difference between the forage components in both areas and thereby also affected the grazing preference. In accordance to our results obtained from the peat area, Bockholt and Buske (1997) observed changes in CP and CF contents in fen growths that could be explained by the physiological stage at the time of sampling. Contrary to our own findings, here the decrease in CP and increase in CF continued till after the middle of July. This might have been explained by the fact that the sampled species in their study were not grazed at all. From the middle of July, our results showed by contrast a grazing-induced improvement in the development of CP and CF. No clear trend in the development of CP was, however, found in a similar study by Hessle et al. (2008) in Sweden, although the sward of the semi-natural grassland site exhibited a comparable species composition. What is noteworthy is that Hessle et al. (2008) found an overall higher content of about 3% CP. These differences in comparison to our results can be ascribed to the adjustment of stocking rate during the Swedish experiment, which was intended to maintain similar sward heights among the different plots. Additionally, the Swedish researchers did not take forage samples from avoided areas, which may also account for the higher CP contents. In the study of Strodthoff (2003), the development of CP and CF was found to be comparable to that of our moraine area. In Strodthoff’s study, just as in ours, the sampling was done on a continuously grazed pasture. However, unlike in our study, there was no similarly strong vegetation gradient. The lack of a comparably distinctive vegetation gradient on the peaty grassland site studied by Strodthoff in connection with the small spatial extent of the experimental area may have prevented the increase of spatial heterogeneity.

**4.4. Herbage digestibility and grazing selectivity**

The average level of digestibility of the pasture growths was higher in the rainy year in 2011 than in the relatively dry experimental period in 2012. However, the pattern of the digestibility of the available pasture growth is different between the two soil types. While after the initial decline in digestibility as a result of the progressive phenological development of the pasture growth in spring, the DOM on the moraine part increased again from about the 12th week, it continued to decrease on the peat soil. This was clearly due to the lack of regrowth and shoot regeneration in the avoided, Carex-dominated peatland vegetation.

For methodological reasons, the evaluation of the selection success cannot be carried out separately according to the site types. The locations of the faecal sample collection for estimating the DOMdiet did not allow conclusions to be drawn about the positions of feed intake. Nevertheless, selection success for digestibility can be seen in sections of Figure 6 where the DOMdiet exceeded the DOMoffer. The grazing animals were only able to achieve selection success at the beginning of the grazing period and thus at a time when the energy contents were high and would therefore not be necessary from a nutritional point of view. In the further course of the grazing period, the grazing animals succeeded in selecting a diet with a significantly higher energy value compared to the average herbage supply in the peat area, but this was not sufficient to reach the level of at least 65% DOMdiet as a precondition for high liveweight gains.

**4.5. Influencing parameters of the liveweight gain**

The overall DLG was 409 g d$^{-1}$ head$^{-1}$ in 2011, 600 g d$^{-1}$ head$^{-1}$ in 2012 and 420 g d$^{-1}$ head$^{-1}$ in 2013. Hessle et al. (2008) reported values of 570 g d$^{-1}$ head$^{-1}$ DLG for grazing heifers, which is only slightly higher than the mean DLG of 500 g d$^{-1}$ head$^{-1}$ in our experiment. Given the higher nutritive value (mean energy content 9.4 MJ ME kg DM$^{-1}$) in the latter study from a Swedish peat soil, we would have expected a larger difference in the DLG. An explanation could be the sward height, which was kept lower than 50 mm by an adjustment of the stocking rate in the Swedish experiment. This measure may have limited the possibility for the grazing animals to enhance the energy intake by selective grazing. The low DLG in our experiment cannot be expected to be sufficient for feasible grazing systems, but are in accordance to those of Breitsameter et al. (2017). They argue that an inadequate balance between herbage on offer and the requirements of the grazing animals resulted in a seasonal pattern of liveweight gains with a minimum in summer. The findings in the current study seem to confirm this hypothesis. Before the 11th week after the 1st of May, the herbage mass exceeded the actual grazed forage and had a high energy content. Later in the grazing season, the average energy content decreased and was even lower in the peat area, where large amounts of herbage mass were still available. From this point on, the heifers were forced to graze in vegetation structures in which no preference patches exist leading subsequently to a more horizontal, layered bite selection as could be seen from the many bitten leaf tips.
The results of the multiple linear regression analysis (Table 4) support these interpretations. The great importance of the digestibility of the (over-standing) forage reserves of the peat part is also reflected in the statistical measures. This, in turn, suggests that even small improvements in the forage quality on the peat areas already should result in a noticeable increase in liveweight gain. Remarkably, the biochemical parameters characterizing the forage value of the moraine growths with their consistently higher feed value indicators do not play an important role for the liveweight gains. However, the amount of forage offered by these swards on the moraine part did. On the one hand, this finding shows the continued suitability of older, species-based and practice-proven assessment schemes of grassland sward quality like the German FVI (Klapp et al. 1953). On the other hand, this is also a clear indication that feed acceptance is a factor not to be underestimated if solutions for higher liveweight gain on semi-natural sites are to be found.

Our results show a strong relationship between the daily liveweight gain (g head$^{-1}$ d$^{-1}$) and the metabolizable energy content (ME MJ kg$^{-1}$ DM$^{-1}$) of the herbage on offer. Nearly 67% of the daily liveweight gain (DLG) was attributable to the energy content of the herbage available for consumption. This trend could also be found for each year separately (Figure 7). However, it should be taken into consideration that the DLG is, besides energy content, also influenced by the available herbage mass, which was the highest in spring when the highest energy contents (MJ ME kg$^{-1}$ DM$^{-1}$) were also observed. The compensatory potential of increase in dry matter intake to counterbalance lower energy contents is obviously limited due to the close relationship between digestibility and herbage intake mediated by rumen filling pressure and gut passage rate. Moreover, the increasing energy and movement expense to realize such a theoretical potential must be regarded as an additional barrier (Abel et al. 1995). If the herbage mass of the moraine area with its high energy content of more than 10 MJ ME kg$^{-1}$ DM$^{-1}$ had not been limited, an overall DLG of 1000 g d$^{-1}$ head$^{-1}$ seems to be achievable: In addition, Mitsch (2009) found similarly high DLG in her grazing experiment with comparable energy contents in the herbage on offer. Therefore, we assume that the increasing spatial heterogeneity seems to limit the DLG at a certain point of spatial distance. The increased costs of selection (movement, energy consumption, leaving the herd) are considered to be the causes why the theoretical potential was not exploited.

4.6. Synthesis

The aim of our research was to investigate to what extent selective grazing behaviour has the potential to compensate for decreasing herbage digestibility in a large-scale spatial context characterized by strong vegetation gradients. Although we were able to observe how this type of grazing behaviour was able to compensate for decreasing feed values, already described by Breitsameter et al. (2017) on a fen site, by a more selective feed intake behaviour, the selection success was clearly limited when only wet grassland communities rich in sedges contributed to the forage supply. Furthermore, in contrast to results from other site contexts (Mezzalira et al. 2012), the heifers were apparently unable to compensate for deficits in the small-scale feeding supply by extending their grazing period. This became particularly apparent in autumn and shows that the shorter day length is a serious limitation when the need for selection is great. The creation of patches as a compensatory measure, which was frequently observed in more suitable plant associations (Distel et al. 1995; Tonn et al. 2019), did not work as hoped here. This can probably be attributed to the inadequate suitability of sedges: they are only bitten in the upper leaf areas, which does not lead to young shoots. In these vegetation contexts, the selection of vegetation available for higher energy density is not realized by small-scale patches, but by a horizontally stratified separation. The limitations of this strategy became apparent in this

\[ DLG = -3208.36 + 408.53 \times ME \]
\[ R^2_{adj} = 0.67 \quad *** \]
\[ SEE = 243.75 \]
study and were also reflected in the development of animal weights. In general, the weight developments were well in line with the dynamics of the digestibility of the growths, which indicates the limited compensatory strength of increased feed intake.

5. Conclusions

Extensive grazing of peaty river valleys for beef production has the potential to generate a very wide range of regulatory and cultural ecosystem services like biodiversity conservation, flooding regulation, soil protection, and appreciation of scenic landscape. However, our study suggests that this requires a site-appropriate and weather-adapted pasture management. With workload-reduced continuous grazing, it is not possible to achieve liveweight gains and carcass qualities that promise a profit. This is also the reason why this form of landscape management is in decline in the glacial landscape of Northeast-Germany. Some simple, but necessary interventions like mobile e-fencing to prevent overgrazing in spring at the moraine flanks and groundwater monitoring wells to ascertain the right time in early summer to restrict grazing to the peat area would suffice to improve land use efficiency without causing other ecosystem services to deteriorate. However, this would require the willingness of nature conservation agencies to give farmers leeway for the adaptation of grazing systems, on the one hand, and also the willingness of the farmers to invest time and effort into the adaptation of the grazing system on the other.

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No potential conflict of interest was reported by the author(s).

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Data availability statement

All relevant data is contained within the manuscript. In addition, raw data from processed data will be made available by the authors, without undue reservation, to any qualified researcher on request.

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