Available online at www.sciencedirect.com
ScienceDirect
ELSEVIER
Applied Animal Behaviour Science 111 (2008) 54–67
APPLIED ANIMAL BEHAVIOUR SCIENCE
www.elsevier.com/locate/applanim

Site use of grazing cattle and sheep in a large-scale pasture landscape: A GPS/GIS assessment

Dorothee Putfarken *, Jürgen Dengler, Stephan Lehmann, Werner Härdtle

Institute of Ecology and Environmental Chemistry, Leuphana University Lüneburg, Scharnhorststr. 1, D-21335 Lüneburg, Germany

Accepted 21 May 2007
Available online 26 June 2007

Abstract

Year-round mixed-species grazing at low densities in large-scale pasture systems has become a popular conservation concept as it is assumed to maintain the valuable biodiversity of semi-open cultural landscapes. This study aims to elucidate which vegetation types are preferentially grazed by cattle and sheep and whether the grazing animals change their preferences through the seasons so that year-round grazing leads to a utilization of all habitats. Additionally, we wanted to determine the main factors underlying the site use patterns of the animals.

The study was conducted on 180 ha of a nature reserve and former military training area in northern Germany from January to October. Within this area, the positions of one cattle herd and one sheep flock were simultaneously recorded every 5 min using the global positioning system (GPS). For this purpose, we fitted one GPS collar alternately to three different cows and another to three different sheep. If the position of a collared animal had changed more than 6 m but less than 100 m within 5 min grazing was assumed based on a validation of these thresholds by direct observation. Using a geographic information system, we analysed the location data with regard to vegetation characteristics, altitude, and distance from fences, water sources, and a sheep shed. For each month, we determined Ivlev's electivity index of both herbivore species in relation to eight broad vegetation types. We used multiple linear regression to create models that describe the grazing frequencies in the grid cells of the area depending on parameters of those grid cells and their spatial position.

Cattle preferred moist and productive habitats, whereas sheep preferred dry and nutrient-poor habitats. Only when feed was in extremely short supply, the animals switched to sites they had previously avoided. Differences in the spatial preferences of the two species were more marked than seasonal changes. Spatial demands of cattle and sheep were largely complementary. Grazing sites with better water availability (i.e. lower distance from the drinking trough and ponds) were significantly preferred by cattle. The sheep preferred grazing sites close to their shed.

* Corresponding author. Tel.: +49 4152 79350; fax: +49 4152 79614.
E-mail address: putfarken@uni-lueneburg.de (D. Putfarken).

doi:10.1016/j.applanim.2007.05.012

Our results show that only a combination of different herbivores guarantees that all habitats of such a large low-intensity pasture are grazed and thus are kept in a management status favourable to conservation. However, the positioning of drinking troughs, fences, and sheds should be carefully considered as these facilities seriously influence the site use of the animals.

Keywords: Feeding electivity; Herbivore; Mixed-species grazing; Nature conservation; Spatial pattern

1. Introduction

In large parts of Europe, modern developments in land cultivation techniques and changes in economic framework have caused considerable losses of valuable open habitats in recent decades (Riecken et al., 2001). On the more productive sites, agriculture has become so intensive that almost all its former positive effects on biodiversity have disappeared (Finck et al., 2002). In marginal areas, by contrast, land that had formerly been used at a low level of intensity has recently become fallow. At the same time, red data books show that a large proportion of threatened species and habitats are concentrated in agricultural landscapes used at low intensities (Korneck et al., 1998; Riecken et al., 2004).

Large-scale pasture landscapes are seen as a suitable strategy to preserve this threatened segment of biodiversity under the framework of current agricultural policy and with limited financial resources (Finck et al., 2002). In contrast to traditional forms of agricultural practice, the objective of large-scale pasture landscapes is to combine both economic and ecological requirements (Härdtle et al., 2002). Grazing at low stocking rates in such large-scale pasture systems is intended to maintain or to create highly diverse ecosystems involving minimal livestock care. Year-round grazing is assumed crucial to keep the pastures in a semi-open state with at most scattered woodland. Additionally, Bakker (1998) postulated that 'multi-species grazing' at low stocking rates may both increase the structural and compositional variation of the vegetation and help to control the encroachment of woody species. Thus, the combination of different herbivore species in large-scale pasture landscapes has become increasingly popular in recent years (e.g. Kampf, 2002).

Previous studies on activity and spatial site-use of grazing animals have focused mainly on economically orientated pasture systems (e.g. Owens et al., 1991; Hart et al., 1993; Dumont et al., 2002). Thus, most of our current knowledge is derived from simple model systems, such as homogeneous pastures of species-poor grasslands, and relatively little detailed work has been done on more complex pasture landscapes with a wide range of different plant communities, at least in temperate lowland environments (Rook and Tallowin, 2003). Furthermore, multi-species grazing may have effects on the vegetation different from that of single-species grazing, as herbivore species differ in diet preferences, terrain use, and their potential to influence vegetation development (Walker, 1994; Bakker, 1998; Rook et al., 2004).

One reason for this lack of information might be that data gathering is the most difficult aspect of all such studies (Turner et al., 2000). Furthermore, a considerable portion of foraging activity takes place at night (Hulbert et al., 1998). Thus, global positioning system (GPS) technology can provide a suitable solution since it allows long-term, uninterrupted monitoring of grazing animals at low cost. However, its use in studies of grazing livestock is still fairly new (Bailey et al., 2004; Schlecht et al., 2004). GPS data, unlike direct observation, also allow easy pairing with numerous spatial parameters stored in a geographic information system (GIS).

Our study is part of a long-term research project that evaluated the effects of large-scale mixed-species grazing on fauna, flora, and vegetation structure of a nature reserve in northern Germany (von Oheimb et al., 2006). Within this framework, we used GPS and GIS methods to analyse the behaviour of cattle (*Bos taurus*) and sheep (*Ovis aries*) over a 10-month period to address the following questions:

- Are there differences in grazing-site preference of the two herbivore species?
- Are there seasonal changes in the use of grazing sites?
- Which are the major factors affecting grazing patterns of cattle and sheep?
- Does year-round mixed grazing with cattle and sheep lead to the desired all-habitat use?

2. Materials and methods

2.1. Study area

The study was carried out in a landscape typical of the lowlands of northern central Europe. It is located in the Höltigbaum Nature Reserve (federal states Schleswig-Holstein and Hamburg, NW Germany, 53°37′N, 10°12′E). The study area is characterised by loamy and sandy glacial deposits. Prevailing soil types are nutrient poor, slightly acidic Luvisols. The climate is of a humid suboceanic type. Mean annual temperature is 8.6 °C (January: 0.5 °C; July: 16.8 °C) and mean precipitation is 770 mm year^{-1} (normal values 1960–1990 for the closest meteorological station Hamburg-Fuhlsbüttel).

The current landscape of the former military training area Höltigbaum (Fig. 1) is the product of past rural and military use. It is characterised by expansive grasslands dominated by *Festuca rubra* agg. and *Agrostis capillaris*. Scattered throughout the area are rows of trees as well as solitary trees, small woods, patches of dry grasslands and sandy heaths as well as some wetlands. After cessation of military use in 1992, trees and bushes started to colonise many areas, and the valuable open landscape began to transform into a landscape of scrubby vegetation.

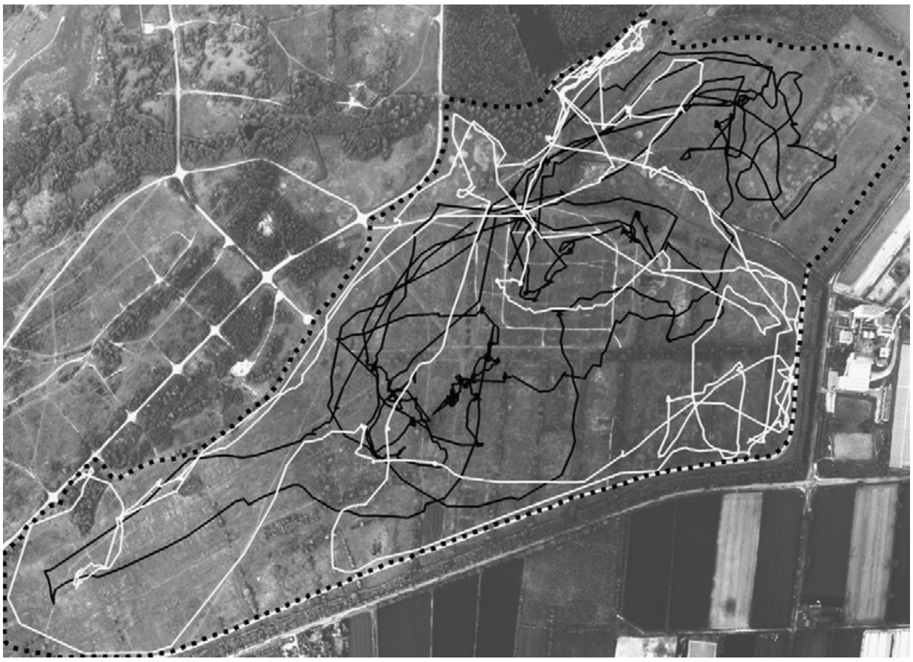

Fig. 1. Aerial photograph of the study area. The delimitation (fence) is marked with black dots. Exemplary tracks of one cow (white line) and one sheep (black line) as inferred from GPS data are superimposed.

2.2. Livestock and management facilities

The study area of 180 ha was fenced off (Fig. 1) and grazed by one herd of cattle and one flock of sheep year-round from April 2000 to October 2003. The cattle herd consisted of red and white lowland cattle, the so-called 'Rotbuntes Niederungsrind', cross-bred with a Galloway bull. The sheep belonged to the resistant race of 'Lüneburg heath sheep', which has low nutritional demands. The livestock was kept at a low density of 0.3 to 0.5 livestock units ha^{-1} (1 LU = 500 kg). On average, there were 74 cattle and 140 sheep, all free to roam throughout the area.

A sheep shed was built as a shelter from extreme weather situations. At the western edge of the pasture, a well was dug and a drinking trough was installed for the cattle.

2.3. Recording of animal positions with GPS collars

To record animal positions we used Garmin eTrex Venture GPS receivers, housed in plastic containers and mounted on collars. Each of the containers was counterbalanced by six external rechargeable 1.2 V/ 7000 mAh accumulators providing sufficient energy to run the GPS units for 7 days. The GPS unit for cattle weighed 2.1 kg, and that used for sheep weighed 1.7 kg. One cow and one sheep were fitted simultaneously with a GPS collar. The animals accepted the GPS collars without any obvious irritation. The GPS collars were changed weekly to recharge the accumulators and to transfer the data. During the study period, three different individuals of each species were alternately used for the tracking.

We chose a logging interval for behavioural data of 5 min. Any interval greater than 5 min may miss data apart from pasture use, such as discrete watering events (Turner et al., 2000). Shorter time intervals would have demanded more frequent collar changes since the receiver's memory is limited to 2047 logging points.

Positions were stored as Gauß-Krüger coordinates of latitude and longitude with information on date, time, and distance from the previous point. We monitored the spatial position of the animals from January to October 2003 resulting in 62,952 position records for the cattle, and 80,672 for the sheep (compare Fig. 1). This corresponds to 218 complete observation days for the cattle and 280 for the sheep.

2.4. Interpretation of GPS records

In order to analyse choice of grazing sites by the animals, we identified and extracted feeding behaviour from the whole GPS data set, which also included resting times and directional movements of the animals. Here, we made two assumptions. On the one hand, according to Porzig and Sambraus (1991) a grazing animal has to move forward to obtain food. When there was no or only slight movement within 5 min, the animal was thus considered to be resting, ruminating, suckling or cleansing itself. Since the accuracy of the GPS receiver is ca. 5 m for complete satellite availability and may be reduced by signal obstruction by canopy cover, two subsequent records almost never have exactly the same plot coordinates even if the receiver is stationary. Accordingly, we assessed the animal's behaviour as 'resting' if the calculated distance within 5 min was less than 6 m. If, on the other hand, an animal moved more than 100 m within 5 min, directional movement was considered to have predominated over grazing. Only time intervals in which the animal moved at least 6 m but less than 100 m were assessed as grazing times and included in the subsequent analyses. Animals' positions caused by human influence, i.e. additional feeding during winter, were also excluded from the analyses. According to these rules, 30,558 (=38%) of the sheep records and 28,141 (=45%) of the cattle records were classified as grazing.

To validate the fixed thresholds of 6 and 100 m, we used a period of direct observation to verify the three behavioural categories inferred from the GPS records. For both herbivore species, we recorded activity every 1 min over 6 days in spring and late autumn. The predominant activity of five such recordings within one GPS time interval, synchronised with the GPS clock, was noted as valid activity. We observed the activities of GPS-monitored cattle over a total of 24.6 h. 94.3% of the direct observations confirmed the behaviour we inferred from GPS data on travelled distances. Activities of GPS-monitored sheep were observed over 23.5 h and they confirmed in 89.4% of all cases the indirectly interpreted activities.

Accordingly, conclusions about animal behaviour derived from GPS data were considered adequately accurate.

We consider the data of the individual collared animals to be representative of their herd or flock since they were always found within their groups at the collar changes and during the direct observation periods.

2.5. Determination of environmental parameters and GIS analysis

2.5.1. General aspects

All recorded positions for the monitored animals were stored in a database (Microsoft Access 2000) and entered into GIS via an SQL connection. For further data analyses, we used the software ArcView 3.1 (ESRI).

To analyse the animals' preferences for certain vegetation types, we constructed a map showing vegetation units classified according to the phytosociological method (cf. Westhoff and van der Maarel, 1973) based on 305 vegetation records made in 2002 and 2003. We distinguished 28 units, largely corresponding to usual phytosociological units. For certain analyses, they were grouped into eight broad types (Table 1). Further, we digitised maps of the cover of woody species (five classes: <5, <25, <50, <75, and $\geq 75\%$) and of elevation. By running a point-in-polygon analysis, every position of a grazing animal was assigned a certain vegetation unit, altitude, and cover class of woody species.

2.5.2. Grid-cell analysis

We subdivided the study area into 3,030 squares with a distance of 30 m between intersections. Prevailing vegetation type was assigned within each grid cell. Using the vegetation records that served as the basis for the vegetation map, we calculated the following average values for each of the 28 vegetation units and assigned these to the respective grid cells: (i) cover of herb layer, cover of cryptogam layer, cover of litter, cover sum of species in the field layer (i.e. herb and cryptogam layer combined); (ii) average height of the herb layer; (iii) evenness of the species composition in the field layer; (iv) cover values of ten characteristic graminoid and herb taxa (*Achillea millefolium*, *Agrostis capillaris*, *Cirsium arvense*, *Deschampsia cespitosa*, *Festuca rubra* agg., *Holcus lanatus*, *H. mollis*, *Poa trivialis*, *Juncus effusus*, *Trifolium repens*); (v) mean indicator values (cover-weighted) for light (L value), soil moisture (F value), soil reaction (R value), and nutrient supply (N value) according to Ellenberg et al. (1991); (vi) a similarly calculated mean indicator value for food quality based on the values given by Briemle et al. (2002). Further,

Table 1
Combination of the mapped plant communities into eight major vegetation types

Major vegetation type	Phytosociological plant communities included	Fraction of study area (%)
Dry and trampled grasslands	*Koelerio-Corynephoretea*, *Polygono-Poetea annuae*, and *Calluno-Ulicetea*	12.8
Nutrient-poor grasslands	Grasslands dominated by *Festuca rubra* agg. (*Molinio-Arrhenatheretea*)	40.0
Mesophytic grasslands	Grasslands dominated by *Agrostis capillaris* and *Cynosurion* communities (both *Molinio-Arrhenatheretea*)	23.8
Wet meadows	Eutraphent vegetation of perennial herbs and moist meadows dominated by *Deschampsia cespitosa*	2.9
Ponds and sedge swamps	Vegetation complexes influenced by water and stands of sedges and rushes (*Magnocaricion*)	1.0
Forests	*Alnus glutinosa* community and *Betulo-Quercetum*	1.8
Small woods and tree groups	Pioneer birch woods, groups of trees, and solitary trees (predominantly oak)	13.9
Others	Different plant communities that occur only on small scales (mostly tall-forb and tall-grass communities)	3.9

every grid square was attributed with information on the number of included vegetation types, on the cover of woody species (see Section 2.5.1) and on elevation. Starting from the centre of each grid square, distances to the cattle trough, to the nearest fence, to the sheep shed, to the nearest pond, and to the nearest woodland were calculated.

2.6. Statistical methods

2.6.1. Preference for vegetation types

We determined monthly grazing frequencies of cattle and sheep for each major vegetation type (cf. Table 1) and related these frequencies to proportions of the study area covered by each vegetation type. Treating the fraction of feeding time as equivalent to the fraction of the respective food type in the herbivore's nutrition, we determined Ivlev's electivity index E_i (Jacobs, 1974). This index is calculated as follows:

$$E_i = \frac{r_i - p_i}{r_i + p_i}$$

with r_i: fraction of feeding time spent in vegetation type i and p_i: fraction of area covered by vegetation type i.

The index E_i takes values between 1 (highly preferred) and -1 (completely avoided). It is 0 when the fraction of feeding time equals the fraction of area covered by the respective vegetation type. It thus enables a more straightforward interpretation than, for example, Chesson's (1983) electivity index $\in_i$, whose value in the case of equity is not fixed.

We tested whether the feeding behaviour of the animals deviated significantly from random grazing (i.e. $E_i = 0$ for all vegetation types) by applying G-tests for the goodness of fit (Sokal and Rohlf, 1995). We calculated the goodness of fit for monthly data as well as pooled over the entire grazing period (G_P), the contribution of differences between the months (heterogeneity, G_H), and, finally, the total value (G_T).

2.6.2. Multiple regression analyses

Relationships between spatial site use by grazing animals and environmental variables potentially affecting the grazing behaviour were analysed with multiple linear regressions (calculated with SPSS, version 14.0). We used grazing frequency per grid cell as the dependent variable ($n = 3030$ grid squares) and the 29 environmental variables available per grid cell (see Section 2.5.2) as predictors. These analyses were carried out separately for both animal species and for winter (January to March) and summer (May to July).

Before conducting the regression analyses, we tested for normality of data distributions for all dependent and predictor variables by use of normal quantile plots (cf. Sokal and Rohlf, 1995). When they markedly deviated, we applied the one transformation (log, square root, cube root, fourth root, arcsin) that resulted in the best approximation to the normal distribution (cf. Quinn and Keough, 2002). From groups of strongly intercorrelated variables ($r > |0.80|$) only one was retained. This led to the omission of the variables cover sum of field layer (r with cover of litter = -0.85; r with cover of *Trifolium repens* = 0.85) and cover of *Holcus mollis* (r with N value = -0.86). The multiple regression was then carried out for the remaining 27 predictor variables in a stepwise forward procedure. The p-to-enter value was set to 0.001 and the p-to-remove value to 0.002 as these values are freely eligible (Sokal and Rohlf, 1995) and we preferred to obtain rather parsimonious models.

3. Results

3.1. Preferences for different vegetation types

The feeding behaviour of both herbivore species deviated significantly from random grazing when the entire investigation period was pooled (cattle: $G_P = 2585$; $n = 28{,}141$; d.f. = 7;

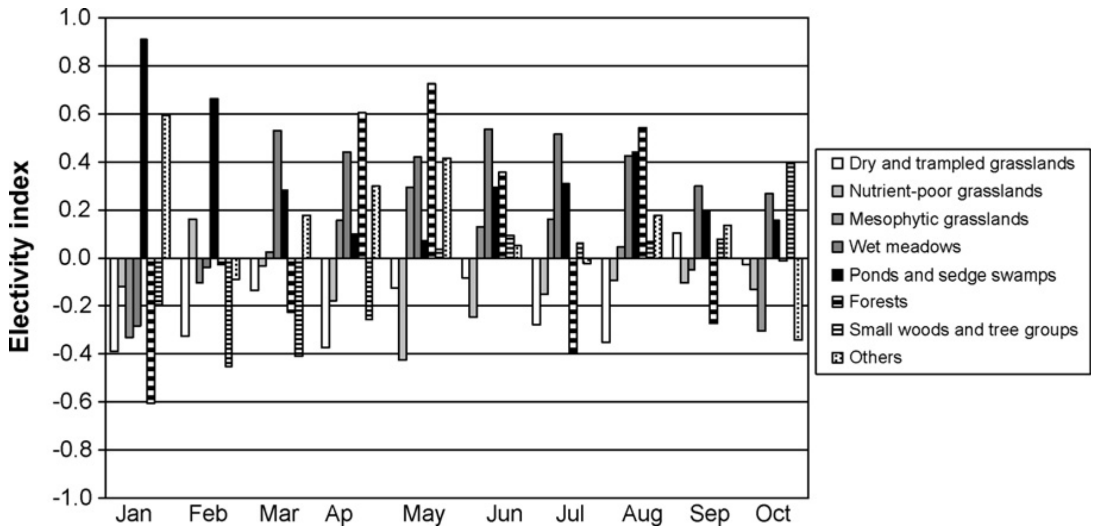

Fig. 2. Ivlev's electivity index E_i for grazing cattle in relation to the eight major vegetation types of Table 1 during the study period in 2003.

$p \ll 0.001$; sheep: $G_P = 2678$; $n = 30{,}558$; d.f. = 7; $p \ll 0.001$) and also for each individual month ($p < 0.001$ throughout).

Site use by cattle showed distinct seasonal changes (Fig. 2; $G_H = 4263$; d.f. = 63; $p \ll 0.001$). Most vegetation types that were used more than average during spring and summer were more or less avoided in winter. However, the cattle moved to poor grasslands, which they had previously avoided in February only, when food was extremely short in supply, and even then, utilization was limited. Ponds and sedge swamps were used instead far more intensively at those times than in other seasons. Year-round bodies of water were of outstanding importance for the cattle. During the growing season, various vegetation types became important for the foraging cattle. Apart from ponds and sedge swamps, the cattle significantly used wet meadows, mesophytic grasslands, and woods.

Preferences of grazing sheep for different vegetation types (Fig. 3) were mostly complementary to those of the cattle. Preferences of cattle and sheep were similar only in

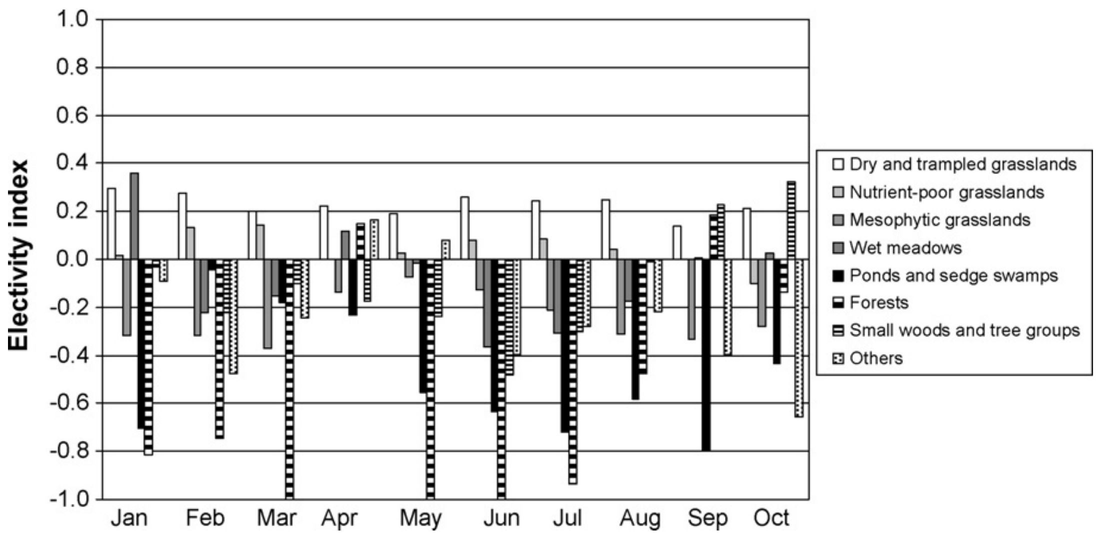

Fig. 3. Ivlev's electivity index E_i for grazing sheep in relation to the eight major vegetation types of Table 1 during the study period in 2003.

autumn. Sheep avoided ponds and sedge swamps during the entire study period, whereas they used dry and poor grasslands more than average almost continuously. Seasonal changes in site use by sheep were less pronounced than with cattle ($G_H = 2177$; d.f. = 63; $p \ll 0.001$). In January, sheep used wet meadows more than average. Nevertheless, there was undiminished use of dry, poor, and trampled grasslands.

3.2. Factors affecting site use by the grazing animals

The multiple regression models explained between one fifth and one half of the feeding behaviour of the two herbivore species in the two time periods (Table 2) indicating that they did

Table 2
Results of the multiple linear regression analyses for grazing preference of the two herbivores during two time periods. The dependent variable in each of the four models is $\log_{10}$ (number of grazing records + 1). The predictor variables are arranged by decreasing absolute values of the standardized partial regression coefficients

Model	r^2	r^2_{adj}	Predictor variables included	Transformation	Standardized coefficient
Cattle in winter (January to March)	0.220	0.218	Distance to drinking trough	Cube root	−0.324
			Distance to fence	Cube root	0.256
			Cover of *Juncus effusus*	Fourth root	0.184
			Distance to sheep shed	Cube root	−0.176
			Mean indicator value for moisture (F)	Log_{10}	−0.142
			Distance to the nearest pond	Square root	−0.089
			Mean indicator value for food quality	–	−0.073
			Number of vegetation types	Square root	0.059
Cattle in summer (May to July)	0.327	0.325	Distance to drinking trough	Cube root	−0.697
			Distance to sheep shed	Cube root	−0.569
			Altitude	–	0.206
			Cover of litter	Fourth root	−0.188
			Distance to the nearest pond	Square root	−0.114
			Mean indicator value for reaction (R)	Log_{10}	−0.097
			Mean indicator value for moisture (F)	Log_{10}	−0.077
			Number of vegetation types	Square root	0.052
Sheep in winter (January to March)	0.417	0.415	Distance to sheep shed	Cube root	−0.367
			Distance to fence	Cube root	0.358
			Cover of *Achillea millefolium*	Log_{10}	−0.234
			Evenness of species composition	–	0.165
			Cover of *Poa trivialis*	Fourth root	−0.146
			Mean indicator value for moisture (F)	Log_{10}	−0.099
			Distance to drinking trough	Cube root	−0.099
Sheep in summer (May to July)	0.496	0.494	Distance to drinking trough	Cube root	−0.622
			Distance to sheep shed	Cube root	−0.462
			Distance to fence	Cube root	0.299
			Altitude	–	0.160
			Mean indicator value for moisture (F)	Log_{10}	−0.094
			Cover of *Holcus lanatus*	Fourth root	0.094
			Distance to the nearest woodland	Square root	0.065

not graze randomly. The explained variance was higher for sheep than for cattle in both seasons and also higher for both species in summer than in winter.

All four models showed high coincidence in the selected variables and their relative importance. Three variables were included in all four models (distance to drinking trough, distance to fence, mean indicator value for moisture) and 'distance to fence' was included in three models. Distance to drinking trough was the strongest predictor variable for cattle in both seasons and for sheep during summer, with the animals preferably grazing in the proximity of the trough. In both species, the spatial arrangement of the whole meadow was far more important for feeding behaviour than were the compositional and structural characteristics of the individual grid cells. None of the included variables changed from positive to negative between species or between seasons.

The preference by cattle for grazing sites near the trough was higher than for sheep in both seasons, and cattle – in contrast to sheep – also showed an increased grazing frequency near ponds. As regards the vegetation composition, cattle preferred heterogeneous patches (positive association with number of vegetation types) in both seasons and additionally stands with *Juncus effusus* in winter.

For the sheep, the importance of the proximity of the drinking trough increased substantially from winter to summer. Species composition played a role in the selection of grazing sites, with places of high cover of *Achillea millefolium* and *Poa trivialis* rather being avoided in winter and those with high cover of *Holcus lanatus* preferably used in summer.

4. Discussion

4.1. Preferences for different vegetation types

The most remarkable outcome of the electivity analyses is that the cattle and sheep foraged among vegetation types almost complementarily. Whereas cattle preferably grazed in communities in wet places (ponds, sedge swamps, and wet meadows), these were for the most part avoided by sheep. Alternately, low growing, unproductive vegetation types of anhydromorphic sites (dry, trampled, and nutrient-poor grasslands) were preferentially grazed by sheep but used less than average by cattle. As regards cattle, our findings are similar to those of Pinchak et al. (1991), who reported that cattle in a large, heterogeneous pasture landscape preferentially foraged in productive (loamy) grasslands, wetlands, and grazable woodlands, but avoided unproductive grasslands (shallow loamy and coarse upland sites).

Much of the complementary feeding behaviour of cattle and sheep may be explained by the animals' different dietary choices. These are driven by factors, such as body size, digestive physiology, and dental anatomy (Walker, 1994; Rook and Tallowin, 2003; Rook et al., 2004). Larger animals have relatively large gut capacity in relation to their metabolic requirements and they can retain digesta in the tract for longer and thus digest it more thoroughly (Illius and Gordon, 1992; Rook and Tallowin, 2003). This means that they can deal with a lower digestibility diet and thus can forage less selectively than smaller animals, which have to select higher-quality items (Illius and Gordon, 1993). On the other hand, larger herbivores need taller swards to subsist than smaller ones do (Illius and Gordon, 1987). Additionally, sheep with their narrow mouths and highly curved incisor arcades are anatomically able to graze much more selectively and closer to the ground than can cattle (Walker, 1994; Rook et al., 2004). Stroh et al. (2004) found that cattle normally only use vegetation above 5 to 10 cm of height.

These aspects together explain why the cattle in the study preferably used moist and wet habitats, where biomass was abundant but of relatively low quality, and avoided low growing, unproductive stands. Bunzel-Drüke (2004) and Bailey (2005) also reported that cattle preferably graze on productive sites with high standing crop, and Bailey et al. (1996) stated that larger herbivores might be forced to select lower-quality diets to maintain intake when forage is limited. The high electivity of the cattle for ponds and sedge swamps in January and February is consistent with the preference of cattle for oligotrophic wet meadows in winter reported by Gordon (1989a,b). According to Gordon, cattle are forced to use these high-grown stands of low nutritional value when available live material in other communities is depleted. In February, when food was in extremely short supply, the cattle in our study also moved to low-grown, poor grasslands, which they avoided in all other months. However, this led to malnourishment, and additional feeding became necessary.

In our study, the sheep fed mainly on dry, poor grassland where biomass was low, but where palatable herbs of high quality occurred in places. This is consistent with Bailey et al. (1996) who concluded that smaller herbivores require less feeding time and thus can spend relatively more time in selecting a high quality diet. For example, Grant et al. (1996) showed that sheep in contrast to cattle selectively foraged on forbs and higher-quality grasses between tussocks of *Nardus stricta* with its low nutritional value.

The preference or avoidance of certain vegetation types as feeding places may have additional reasons beyond food quality and quantity, such as thermoregulation (cf. Morand-Fehr and Doreau, 2001). The high electivity of cattle for forest patches in the summer months whereas this vegetation type was avoided during the cooler seasons can be explained by the search for shade. Bailey (2005) reported a similar seasonal change in the affinity of cattle to shade trees in California. Sheep, by contrast, avoided forests and even small woods almost completely through most of the year. Obviously, they had no physiological need to avoid strong insolation. Only in April and September sheep frequented woods more than average to feed on geophytes or acorns.

4.2. Factors affecting site use by the grazing animals

Generally, site use by both cattle and sheep was primarily affected by the position of management facilities. Bailey et al. (1998) point out that one of the most important factors determining the selection of feeding places by herbivores is the reduction of travelling distance. Thus, the strategic placement of management facilities that are necessary for the survival or comfort of the animals, such as drinking troughs, sheds, or salt supplies, is an efficient means of increasing or decreasing the grazing pressure in certain parts of a pasture landscape (Bailey et al., 1998; Bailey, 2004).

The regression analyses clearly show that for cattle, water availability was a crucial factor in their choice of feeding places as in both seasons the proximity to the drinking trough was the most influential parameter, and the proximity to the nearest pond was also included in both regression models. Generally, intense cattle grazing is reported around water sources (Owens et al., 1991; Pinchak et al., 1991; Hart et al., 1993).

For sheep, the regression analyses revealed the proximity to their shed as most important parameter. Actually, the sheep often used their shed as a resting place, particularly during winter, when days were short. Being light-active (Porzig and Sambraus, 1991), they did not roam over long distances, but grazed within a close radius of their shed.

Proximity to the cattle's drinking trough also was highly positively correlated with sites preferentially grazed by sheep, as was the proximity to the sheep shed to the sites preferentially grazed by the cattle. These results are astonishing as both facilities were not usable for the respective other herbivore species. Moreover, the sheep satisfied their water requirements by food intake and dew. Thus, the positive correlations of the cattle's feeding places with a specific facility for the sheep and of the sheep's feeding places with a specific facility for the cattle may be caused by curiosity. The reason for preferential grazing at higher distance from the fence may be explained for the sheep by the fact that they prefer dry grasslands (see Section 4.1), which are more abundant in the central parts of the study area.

At first glance, it seems surprising that only few parameters of the actual vegetation were included in the regression models and that these were rather similar for both species whereas the electivity analyses revealed almost complementary preferences of the two animal species for different vegetation types. However, this can be attributed to the different spatial resolution of the two analytical approaches. Whereas in the electivity study point data were used, the regression analyses required grid cells and the assignment of prevailing vegetation type to each. As most grid cells consisted of more than one vegetation type, a grid-based approach inevitably led to an underestimation of effects of vegetation parameters in the regression models. Nevertheless, the regression analysis found that cattle preferably graze in places with high cover of *Juncus effusus* during winter, which is consistent with their notably high electivity for ponds, and sedge swamps in winter months (see Fig. 2). *Juncus effusus* has a low nutritional value but during January and February there were 15 days of snow-cover when this rush species was the only visible green feed. The preference of sheep (during summer) to graze sites with high cover of *Holcus lanatus* is consistent with the findings reported by Bakker (1998).

4.3. Achievement of the conservation goals

After 5 years of year-round mixed-species grazing with cattle and sheep, the Höltigbaum nature reserve has maintained its high structural diversity, and the species richness and abundance of many endangered plant and animal taxa has even increased (von Oheimb et al., 2006). Though there were minor changes in vegetation types, their proportions essentially remained the same (von Oheimb et al., 2006). In particular, the vast number of tree and shrub seedlings that could germinate every year and which otherwise would have led to a considerable increase of woodland cover, were largely damaged or killed by the herbivores (von Oheimb et al., 2006). These positive effects clearly can be attributed to the applied grazing regime.

The grazing preferences of cattle and sheep proved to be complementary in an ideal way. Thus, grazing by either cattle or sheep would not be sufficient to prevent all parts of such a diverse pasture landscape from accumulating litter and becoming fallow. Consequently, a suitable combination of grazing animals appears to be crucial to achieve a sufficient defoliation of the ground vegetation in heterogeneous large-scale pasture landscapes. Previously, the combination of cattle and horses has been particularly suggested for multi-species grazing because of the different foraging strategies of these two herbivores (Bakker, 1998; Bunzel-Drüke, 2004; Reisinger, 2004)—but as shown in our study the combination of cattle and sheep is also suitable.

Our finding of seasonal spatial changes in feeding behaviour suggests additional positive effects on conservation in grasslands may arise from year-round grazing. Together with the interspecific differences, this seasonality reduced the risk of any one part of a pasture landscape being over- or undergrazed. Kämmer (2004) and Reisinger (2004) point out that desired grazing effects may not be seen in some areas except in winter, when feed is in short supply elsewhere. For example, herbivores normally refrain from feeding on *Juncus effusus* with its low nutritional value, and this meadow weed consequently would increase in cover (see Bakker, 1998; Piek, 1998). In our study, however, we found that cattle in times of snow-cover even preferentially fed on *Juncus effusus*, as there were no available alternatives then.

Clearly, the effects of a grazing regime depend on stocking rates relative to the productivity of the site (Reisinger, 2004). If the stocking rates are too low, the herbivores may not be able to keep the landscape open. On the other hand, if the stocking rates are too high, this may result in a homogenising of the vegetation pattern (Bakker, 1998; Bailey, 2004), which is not in accordance with nature-conservation objectives. In our study, 0.3–0.5 LU ha^{-1} appeared to be more or less adequate for vegetation development during the first 3 years after the establishment of the pasture landscape. This is consistent with the proposals for year-round grazing by Piek (1998: 0.2 LU ha^{-1} in heathlands and 0.33 LU ha^{-1} in wet grasslands), Kämmer (2004: 0.3–0.6 LU ha^{-1} in semi-open pasture landscapes), and Reisinger (2004: up to 0.4 LU ha^{-1} for cattle only and 0.6 LU ha^{-1} for multi-species grazing on sites with intermediate productivity).

5. Conclusion

On condition that stocking rates are low, year-round mixed grazing by cattle and sheep appears to be suitable for the conservation of diverse pasture landscapes since both species have complementary feeding preferences, and these also show seasonal changes. As drinking troughs, fences, and sheds proved to influence the selection of grazing sites by herbivores considerably, the placement of such management facilities should be carefully considered.

Acknowledgements

We are indebted to two anonymous referees, whose comments led to considerable improvements of the manuscript, and to Linda Froome-Döring and Curtis Björk for the linguistic revision of the text. The financial support of the German Federal Agency for Nature Conservation (BfN) is gratefully acknowledged.

References

Bailey, D.W., 2004. Management strategies for optimal grazing distribution and use of arid rangelands. J. Anim. Sci. Suppl. 82, E147–E153.

Bailey, D.W., 2005. Identification and creation of optimum habitat conditions for livestock. Rangeland Ecol. Manage. 58, 109–118.

Bailey, D.W., Dumont, B., WallisDeVries, M.F., 1998. Utilization of heterogeneous grasslands by domestic herbivores: theory to management. Ann. Zootech. 47, 321–333.

Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M., Sims, P.L., 1996. Mechanisms that result in large herbivore grazing distribution patterns. J. Range Manage. 49, 386–400.

Bailey, D.W., Keil, M.R., Rittenhouse, L.R., 2004. Research observation: daily movement patterns of hill climbing and bottom dwelling cows. J. Range Manage. 57, 20–28.

Bakker, J.P., 1998. The impact of grazing on plant communities. In: WallisDeVries, M.F., Bakker, J.P., van Wieren, S.E. (Eds.), Grazing and Conservation Management, Conservation Biology Series 11. Kluwer, Dordrecht, pp. 137–184.

Briemle, G., Nitsche, S., Nitsche, L., 2002. Nutzungswertzahlen für Gefäßpflanzen des Grünlandes. In: Klotz, S., Kühn, I., Durka, W. (Eds.), BIOLFLOR – Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schriftenr. Vegetationskd. 38, 203–225.

Bunzel-Drüke, M., 2004. Ersatz für Tarpan und Auerochse – Chancen und Grenzen beim Einsatz von Pferden und Rindern in Wildnisgebieten. Schriftenr. Landschaftspflege Naturschutz 78, 491–510.

Chesson, J., 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64, 1297–1304.

Dumont, B., Carrère, P., D'Hour, P., 2002. Foraging in patchy grasslands: diet selection by sheep and cattle is affected by the abundance and spatial distribution of preferred species. Anim. Res. 51, 367–381.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobot. 18, 1–248.

Finck, P., Riecken, U., Schröder, E., 2002. Pasture landscapes and nature conservation—new strategies for the preservation of open landscapes in Europe. In: Redecker, B., Finck, P., Härdtle, W., Riecken, U., Schröder, E. (Eds.), Pasture Landscapes and Nature Conservation. Springer, Berlin, pp. 1–13.

Gordon, I.J., 1989a. Vegetation community selection by ungulates on the Isle of Rhum. II. Vegetation community selection. J. Appl. Ecol. 26, 53–64.

Gordon, I.J., 1989b. Vegetation community selection by ungulates on the Isle of Rhum. III. Determinants of vegetation community selection. J. Appl. Ecol. 26, 65–79.

Grant, S.A., Torvell, L., Sim, E.M., Small, J.L., Armstrong, R.H., 1996. Controlled grazing studies on Nardus grassland: effects of between-tussock sward height and species of grazer on Nardus utilization and floristic composition in two fields in Scotland. J. Appl. Ecol. 33, 1053–1064.

Härdtle, W., Mierwald, U., Behrends, T., Eischeid, I., Garniel, A., Grell, H., Haese, D., Schneider-Fenske, A., Voigt, N., 2002. Pasture landscapes in Germany—progress towards sustainable use of agricultural land. In: Finck, P., Härdtle, W., Riecken, U., Schröder, E. (Eds.), Pasture Landscapes and Nature Conservation. Springer, Berlin, pp. 147–160.

Hart, R.H., Bissio, J., Samuel, M.J., Waggoner, J.W., 1993. Grazing systems, pasture size, and cattle grazing behaviour, distributions and gains. J. Range Manage. 46, 81–87.

Hulbert, I.A.R., Wyllie, J.T.B., Waterhouse, A., French, J., McNulty, D., 1998. A note on the circadian rhythm and feeding behaviour of sheep fitted with a lightweight GPS collar. Appl. Anim. Behav. Sci. 60, 359–364.

Illius, A.W., Gordon, I.J., 1987. The allometry of food intake in grazing ruminants. J. Anim. Ecol. 56, 989–999.

Illius, A.W., Gordon, I.J., 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. Oecologia 89, 428–434.

Illius, A.W., Gordon, I.J., 1993. Diet selection in mammalian herbivores: constraints and tactics. In: Hughes, R.N. (Ed.), Diet Selection: an Interdisciplinary Approach to Foraging Behaviour. Blackwell Scientific, Oxford, pp. 157–181.

Jacobs, J., 1974. Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's electivity index. Oecologia 14, 413–417.

Kämmer, G., 2004. Veterinärmedizinische, rechtliche, finanzielle und praktische Aspekte bei der großflächigen Extensivhaltung von Rindern – Erfahrungen aus der Halboffenen Weidelandschaft Schäferhaus. Schriftenr, Landschaftspflege Naturschutz 78, 377–392.

Kampf, H., 2002. Nature conservation in pastoral landscapes: challenges, changes and constraints. In: Redecker, B., Finck, P., Härdtle, W., Riecken, U., Schröder, E. (Eds.), Pasture Landscapes and Nature Conservation. Springer, Berlin, pp. 15–38.

Korneck, D., Schnittler, M., Klingenstein, F., Ludwig, G., Takla, M., Bohn, U., May, R., 1998. Warum verarmt unsere Flora? Auswertung der Roten Liste der Farn- und Blütenpflanze Deutschlands. Schriftenr. Vegetationskd. 29, 299–444.

Morand-Fehr, P., Doreau, M., 2001. Effects of heat stress on feed intake and digestion in ruminants. Prod. Anim. 14, 15–27.

Owens, M.K., Launchbaugh, K.L., Holloway, J.W., 1991. Pasture characteristics affecting spatial distribution of utilization by cattle in mixed brush communities. J. Range Manage. 44, 118–123.

Piek, H., 1998. The practical use of grazing in nature reserves in The Netherlands. In: WallisDeVries, M.F., Bakker, J.P., van Wieren, S.E. (Eds.), Grazing and Conservation Management, Conservation Biology Series 11. Kluwer, Dordrecht, pp. 253–272.

Pinchak, W.E., Smith, M.E., Hart, R.H., Waggoner, J.W., 1991. Beef cattle distribution patterns on foothill range. J. Range Manage. 44, 267–275.

Porzig, E., Sambraus, E.E., 1991. Nahrungsaufnahmeverhalten landwirtschaftlicher Nutztiere. Deutscher Landwirtschaftsverlag, Berlin.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge.

Reisinger, E., 2004. Ausgewählte naturschutzfachliche und sozioökonomische Anforderungen für die Etablierung großflächiger Weidesysteme. Schriftenr. Landschaftspflege Naturschutz 78, 469–489.

Riecken, U., Finck, P., Härdtle, W., 2004. Weidelandschaften und Wildnisgebiete: Vom Experiment zur Praxis – eine Einführung. Schriftenr. Landschaftspflege Naturschutz 78, 9–19.

Riecken, U., Schröder, E., Finck, P., 2001. Halboffene Weidelandschaften und Wildnisgebiete als Ziele des Naturschutzes aus Bundessicht – Alternativen zum Erhalt und zur Pflege von Offenlandbiotopen. In: Gerken, B., Görner, M. (Eds.), Neue Modelle zu Maßnahmen der Landschaftsentwicklung mit großen Pflanzenfressern – Praktische Erfahrungen bei der Umsetzung. Natur- und Kulturlandschaft 4, Höxter, pp. 88–94.

Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M.F., Parente, G., Mills, J., 2004. Matching type of livestock to desired biodiversity outcomes in pastures—a review. Biol. Conserv. 119, 137–150.

Rook, A.J., Tallowin, J.R.B., 2003. Grazing and pasture management for biodiversity benefits. Anim. Res. 52, 181–189.

Schlecht, E., Hülsebusch, C., Mahler, F., Becker, K., 2004. The use of differentially corrected global positioning system to monitor activities of cattle at pasture. Appl. Anim. Behav. Sci. 85, 185–202.

Sokal, R.R., Rohlf, F.J., 1995. Biometry—The Principles and Practice of Statistics in Biological Research, 3rd ed. Freeman, New York.

Stroh, M., Kratochwil, A., Schwabe, A., 2004. Fraß- und Raumnutzungseffekte bei Rinderbeweidung in halboffenen Weidelandschaften: Leitbildflächen und Restitutionsgebiete im Emsland, (Niedersachsen). NNA-Ber. 17, 133–146.

Turner, L.W., Udal, M.C., Larson, B.T., Shearer, S.A., 2000. Monitoring cattle behaviour and pasture use with GPS and GIS. Can. J. Anim. Sci. 80, 405–413.

von Oheimb, G., Eischeid, I., Finck, P., Grell, H., Härdtle, W., Mierwald, U., Riecken, U., Sandkühler, J., 2006. Halboffene Weidelandschaft Höltigbaum – Perspektiven für den Erhalt und die naturverträgliche Nutzung von Offenlandlebensräumen. Naturschutz Biol. Vielfalt 36, 1–280 + CD-ROM.

Walker, J.W., 1994. Multispecies grazing: the ecological advantage. Sheep Res. J. Spec. Issue 52–64.

Westhoff, V., van der Maarel, E., 1973. The Braun-Blanquet approach. In: Whittaker, R.H. (Ed.), Ordination and Classification of Communities. Handbook of Vegetation Science 5, Junk, The Hague, pp. 617–726.