Ministerie van Verkeer en Waterstaat

Directoraat-Generaal Rijkswaterstaat

Directie IJsselmeergebied

Intern rapport

Habitat use and the social structure of a herd of Heck cattle in the Oostvaardersplassen

door E. van Adrichem

1994 -13 lio

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Interne rapporten zijn in principe interne communicatiemiddelen; hun inhoud varieert sterk en kan zowel betrekking hebben op een weergave van cijferreeksen, als op een discussie van onderzoeksresultaten.

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Referaat

Terrein gebruik en sociale organisatie van Heckrunderen in de Oostvaardersplassen III / door E. van Adrichem; Ministerie van Verkeer en Waterstaat, Rijkswaterstaat, Directie IJsselmeergebied - Lelystad : RWS, FL, 1993. - 40 p. : fig., tab., bijl. : 21c x 29.7c. - (Intern rapport / Directie IJsselmeergebied: 1994 - 13 Lio)

Dit rapport bevat een gedeelte van het onderzoek naar het terreingebruik van Heckrunderen in de Oostvaardersplassen. Stieren bevinden zich in stiergroepen die zich tot een relatief klein gebied van het terrein beperken, terwijl koeien en onvolwassen beesten van het hele terrein gebruik maken. Om tot mogelijke verklaringen te komen van de verschillen in terreingebruik tussen de beide sexen is er gekeken naar de voedselkwaliteit van verscheidene vegetatie-typen, en de foerageertijd en vegetatie-type selectie van stieren en koeien. Verder is de tijdsbesteding en het gedrag van stieren in stiergroepen vergeleken met de tijdsbesteding en het gedrag in aanwezigheid van koeien.

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Acknowledgements

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Abstract

This study describes the patterns of habitat use, vegetation type selection and activity budgets of bulls and cows from a population of free ranging Heck cattle, during the spring of 1992 in the Oostvaardersplassen.
Bulls form bullgroups that confine themselves to certain areas of the study area, while cows, who form a herd with subadults and calves, roam throughout the area.
Forage samples of six vegetation types that occur in the study area were related to the different requirements of bulls and cows with regard to crude protein and digestible organic matter. These do not fall below maintenance demands for both sexes.
Cows much more time grazing then bulls and preferentially selected the open grassland vegetation types (65.9 % of foraging observations). Bulls showed a broader selection, including the grassland-reed vegetation. Both sexes avoided the vegetation types with high reed abundance.
Bulls from the different bullgroups spent an equal amount of time with individuals from the main herd, and also spent an equal amount of time on basic activities when they were in a bullgroup or when mingling with the main herd.
As forage quality and quantity are relatively high for most part of the year it is suggested that the formation of bullgroups is foremost a mating strategy. This is supported by the fact that bullgroups spent more time on interactions among each other in the absence of the main herd.

1. INTRODUCTION

Grazing by free ranging herbivores as a management tool for nature conservation has become increasingly popular in the Netherlands over the past twenty years (Vulink & Drost 1991 b, Huijser 1992). The effects of grazing in altering vegetational structure, diversity and productivity have since been a subject of much attention and research (e.g. Putman 1986, Thalen 1987). These effects largely depend upon the species of herbivores, number of animals (grazing pressure) and continuity (e.g. seasonal variation). Grazing regimes in nature reserves vary according to the different objectives or the desired effects by local management authorities. In several larger nature reserves in the Netherlands large herbivores have been (re-)introduced, assuming that they play a key role in the functioning of an ecosystem and contribute to self regulation (Thalen 1987), thereby minimizing human interference in these reserves.

The Oostvaardersplassen (OVP) is an eutrophic wetland of 5600 ha and is located in the province of South Flevoland, in the centre of the Netherlands. It originated in 1968 as a consequence of the creation of the new province and within a short time it became an important area for (migrating) waterfowl and birds of prey. Because of the rapid succession of reed (*Phragmitis australis*), willow (*Salix spp.*) and elder (*sambucus nigra*) various management techniques have been applied in the OVP to maintain it as a suitable habitat for different bird-species (Vulink & Drost 1991 b). These techniques included water level control of the marsh part (3700 ha), and sowing, mowing and seasonal grazing by domestic livestock in the terrestrial part (1900 ha).

In 1983/4 small populations of free ranging Heck cattle and Konik horses were introduced in a compartment of 500 ha in the dry part (Blaakmeer *et al.* 1992) as a first attempt to create and maintain open grasslands without human interference on a year round basis grazing regime. By October 1988 these populations had grown to 80 and 60 individuals, respectively. The area was expanded to 650 ha and all additional management activities in this area were put to a halt. Fifteen Heck cattle were added to the herd and in the following two years the herd almost doubled in size and distinct groups started to form.

In June 1991 a research project was initiated for the duration of one year aimed at the following questions; what is the social structure of the herd of Heck cattle and what are the effects of this structure upon the use of the area? Studies conducted in the summer of 1991 (Blaakmeer *et al.* 1992) and in the winter and spring of 1992 (Kooi *et al.* 1992) indicated that the herd of Heck cattle could be classified into three social groups that persist throughout the year;

1. a main herd consisting of bulls, cows, sub-adults and calves;
2. several groups of adult bulls;
3. solitary bulls (adult).

The observed social structure has led to differences in habitat use between the sexes whereby the home range of the main herd covers almost half of the habitat, and the bull groups and solitary bulls occupy smaller home ranges throughout the year in different parts of the area.

Sexual segregation is common among North and South temperate ungulates and has been investigated among a number of species (Main & Coblentz 1990, Clutton-Brock *et al.* 1987). The phenomena of territorial bull groups in free ranging (primitive) cattle has also been described by Hall (1988) for Chillingham cattle. Sex differences in habitat use are generally believed to occur as a result of different energetic requirements and/or reproductive strategies between the sexes (cit.in Main & Coblentz, 1990). This study is part of the research project and the aim is to find possible explanations for the formation of bull groups with rising population density in the OVP. For this the following hypotheses have been formulated:
1 Differences in requirements for energy and nutrients between bulls and cows lead to different patterns of habitat use.
2 The association of adult bulls in smaller groups is a strategy to minimize competition and thus enhance reproductive success

In the case of species where male body size is larger than that of females, as in Heck cattle, different requirements arise whereby males require absolutely more food and females have higher nutrient requirements, because of their smaller body size and the high costs of gestation and lactation (Clutton-Brock *et al.* 1987, Gosling 1986). Therefore the first hypothesis adresses the question whether the different patterns of habitat use between the sexes are a consequence of different foraging behaviour, because males will make a selection for quantity and females a selection for quality. These differences should be reflected in the daily maintenance requirements for bulls and lactating cows, which can then be related to forage quality, vegetation type selection and foraging time.
The second hypthesis was formulated because to enhance reproductive success males can either follow females or sit and wait for females to arrive. Which strategy depends on the densities and movements of females, and the abundance and quality of resources (Gosling 1986). The formation of bull groups that confine themselves to a certain area in the OVP can be regarded as a 'sit and wait' strategy or resource defence territoriality (Gosling 1986). Establishing small territorial bull groups could avoid high levels of disturbance and decreasing reproductive success associated with the rising numbers of male competitors in the main herd. Therefore the time spent on basic activities and social behaviour for bulls were compared in the presence and absence of cows.

2. MATERIAL AND METHODS

2.1 Study area

The area in the OVP where the populations of free ranging Heck cattle and Konik horses have been introduced is generally referred to as the 'year-round grazing area'. It consists of 650 ha and has been divided into a grid of 127 compartments (av. size 6.25 ha, see Appendix 1). In January 1992 some 170 cattle and 90 horses roamed the area. Prior to October 1988 c.300 ha of natural reed/willow vegetation had been converted into open grassland of which about one-third was rapidly overgrown with reed again.

Eight different vegetation types have been distinguished on the basis of abundance of characteristic species in permanent plots (Braun-Blanquet method - A. Smit 1991 a,b). The vegetation types are described below and are shown in figure 1, overleaf (see also appendix II) .

Table 1. Main vegetation types within the study area

VEGETATION TYPE (code)	AREA (ha)	MOST ABUNDANT PLANT SPECIES
Grassland dry G1	34	*Lolium perenne, Poa trivialis, Trifolium repens*
Grassland wet G2	52	*Festuca rubra, Phleum pratense Poa trivialis, Agrostis*
Grassland-reed PG1	60	*Poa trivialis,Phleum pratense Lolium perenne,Trifolium repens Phragmitis australis*
Grassland-reed PG2	29	*Poa trivialis, Festuca rubra Phragmitis australis*
Grassland-reed PG3	8	*Lolium perenne,Phleum pratense Phragmitis australis*
Reedland-grass PH2	80	*Phragmitis australis,Poa trivialis cirsium spp.*
Reedland PH	20	*Phragmitis australis*
Reedland-rough growth GR2	355	*Phragmitis australis, Sambucus nigra,Salix spp. Poa trivialis, Urtica dioica*

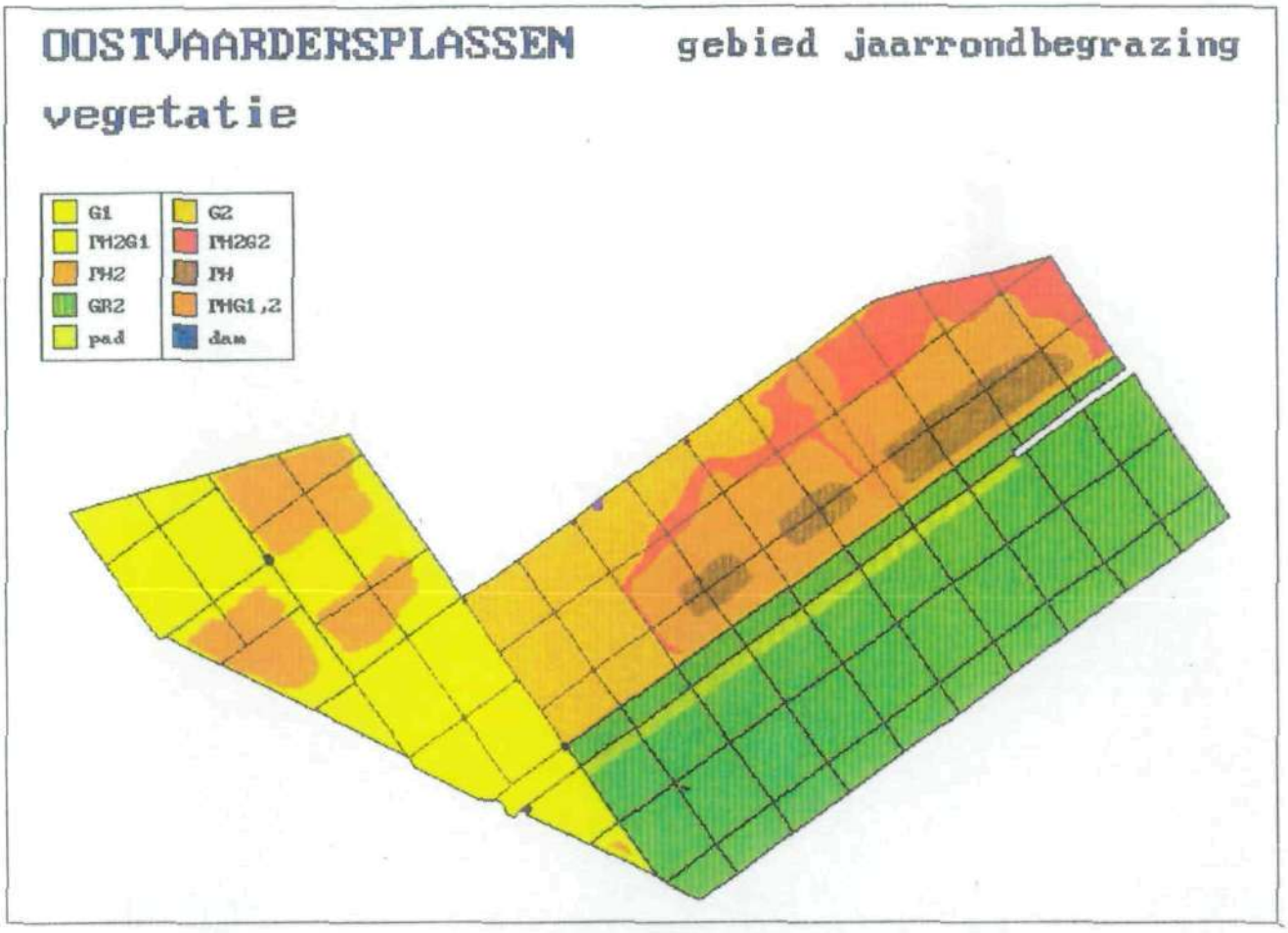


Fig. 1. Vegetation map of the study area

NOTE:

G1 and G2 are also defined as 'open grasslands'
PG2 has much denser stands of reed than PG1 (A. Smit 1992a).
'Path' is very short vegetation and consists mainly of *Poa trivialis.*
'Dam' is bare earth.
GR2 compartments south of 'path' consists of approximately 65 % reed. This area is also referred as the 'stort'. The dams, ponds and path vegetation make up the remainder 12 ha of the area.

2.2 Field methods

The study was carried out from the end of April until the beginning of July 1992. Due to the removal of 25 individuals in February the herd consisted of approximately 150 animals: 44 adult bulls, 45 adult cows, and sub-adults and calves. Bulls are considered adult from the age of four years, cows at approximately one and a half year. All adult and most sub-adult cattle were identified and recognized individually (Blaakmeer *et al.* 1992).

The social groups are defined as follows:

Main herd	cows, calves and sub-adults (including bulls up to 4 years):
Bull groups	association of adult bulls into groups sharing a home range:
Solitary bulls	adult bulls that roam alone .

Four different bull groups were distinguished and six representative bulls from these groups were each observed continuously for six days. By alternating the days for the bulls each bull was observed over the whole period. The days were divided into 3 mornings (06.00 - 14.00) and 3 evenings (14.00 - 22.00) per bull. Total observation time amounts to 14,981 minutes (250 hrs.).
In addition six different lactating cows from the main herd were observed for one day each for a total of 2,493 minutes (42 hrs.). Two night watches (one bull and one cow) were done towards the end of the observation period and scans (methodology specified in Blaakmeer *et al.* 1991) were continued once a week. The animals were used to the presence of observers and could be followed on foot at short distances without disturbance.

During the continuous observations the following data relating to the focal animal were recorded (described in Appendix III): location and vegetation type; social group; number of animals in the group; activity; interactions; opponent; reactions of the opponent; guarding a cow (for bulls) and suckling calf (for cows).The time was noted to the nearest minute each time a change in one of the events mentioned above took place. Every thirty minutes a five minute protocol of the focal animal was made. During these protocols all activities and interactions were recorded every 10 seconds, including step rates. Of these protocols, only grazing protocols for bulls were analyzed, during which bite rates and forage plant selection were recorded.

Forage samples (simulating bites) were taken once a month and the following contents were determined:

1. Neutral Detergent Fibre (cell wall %);
2. total Kjedahl nitrogen (crude protein %);
3. the in-vivo organic matter digestibility (DOM %).

Applied methodologies are specified in Vulink & Drost (1991 a).

2.3 Data analysis

Differences in energy and nutrient requirements for the same species are generally attributed to differences in body size (see introduction and discussion). In the case of Heck cattle a literature review (see Table 1) was conducted to obtain data for differences between the sexes for daily requirements.

Bull weights vary between 600-1000 kg and cows between 300-500 kg. (Van der Ouderaa, pers. comm.). Therefore the average weight for bulls was set at 800 kg and for cows at 400 kg. Daily requirements of bulls and lactating cows for energy, dry matter intake, protein and digestibility are given in Table 2 .

Table 2. Daily requirements for bulls and lactating cows.

	Bulls	Cows
Metabolizable Energy (kcal)[1&2]	32000	25000
Crude Protein %[1]	4.2	7.8
Dry Matter (kg/day)[2]	20	10
Digestible Organic Matter (DOM)%[3]	50	76

NOTE:
[1] Agricultural Research Council (ARC 1980)
[2] Vulink & Drost (1991 a)
[3] H.H.T. Prins (1987).

[1] Mean metabolizable gross energy forage (ME, 2.3 kcal/kg DM): q = 0.5. Energy requirements are multiplied by 1.2 for free ranging cattle.
For bulls the figures for metabolizable energy and crude protein were derived from tables 3.19 and 4.13 in ARC 1980, respectively (weight gain 0.75 kg, extrapolation to 800 kg) and for cows tables 3.28 and the intermediate of tables 4.23 and 10.5 (weight gain 0.25 kg, the comparison was made with lactating Jersey cows weighing 400 kg).

[2] Dry matter intake: 0.025xW (W = body weight).

[3] DOM% (dry ash weight): ME (J) = 15.06 * DOM (g), divided by 0.9 to correct for organic DOM%.

The results for the analysis of data collected for the bulls are presented in the following way:

*bulls	the 6 observed bulls together, representing all the bulls in the area
*bull groups	the observed individual bulls from the bull groups are regarded as representing their bull group (**)
*individual bulls	each individual bull has been given a number
*cows	the six different cows together, representing all the cows in the study area (***)
*mixed herd	when the main herd (2.2) passes or temporarily stays in the homerange of a bull group (called visiting) and the bulls mingle amongst the cows the bulls (or bull groups) and cows are said to be in a mixed herd

** bull no.55 was initially regarded as a solitary bull, however after two observation days he rejoined his former bull group (Blaakmeer *et al.*, Kooi *et al.*, 1992). These two days have been omitted when analyzing 'bull groups'.
*** in several analyses (marked -2) only four of the six cows are represented because their daily range movement on the two observation days were markedly different from the normally observed range by the main herd (Blaakmeer *et al.* 1992, Kooi & Rademaker 1992, pers. obs.).

Using ILWIS Geographic Information System (ITC Enschede) the vegetation map of the year-round grazing area was digitized giving the exact coverage (in ha) of the vegetation types. This was used to calculate the use and selection of the different vegetation types. Aerial photographs that were available for digitizing did not include all the compartments with GR2 vegetation (Appendix 1).

To analyze the vegetation type selection for the focal animals, the selection index (E) (Jacobs 1974 cit. in Gordon 1989 b) was used, which is calculated as follows:

$$E = (Ui - Ai)/\{(Ui + Ai) - [2*(Ui*Ai)]\}$$

where Ui is the proportion of time spent grazing on vegetation type i and Ai is the proportion of the study area occupied by vegetation type i. The value of E ranges between -1 to +1;
-1 to 0 indicates an avoidance of the vegetation type and 0 to +1 a preference of that vegetation type. GR2 is not included in this calculation because the exact coverage of the grass and forb vegetation among the reed could not be estimated.
Given the small sample size and the fact that most of the recorded data were not normally distributed, nonparametric statistical tests were applied (Siegel 1956) using SX and SPSS statistical computer programs.

3. RESULTS

3.1 Biochemical composition and digestibility of forage plants.

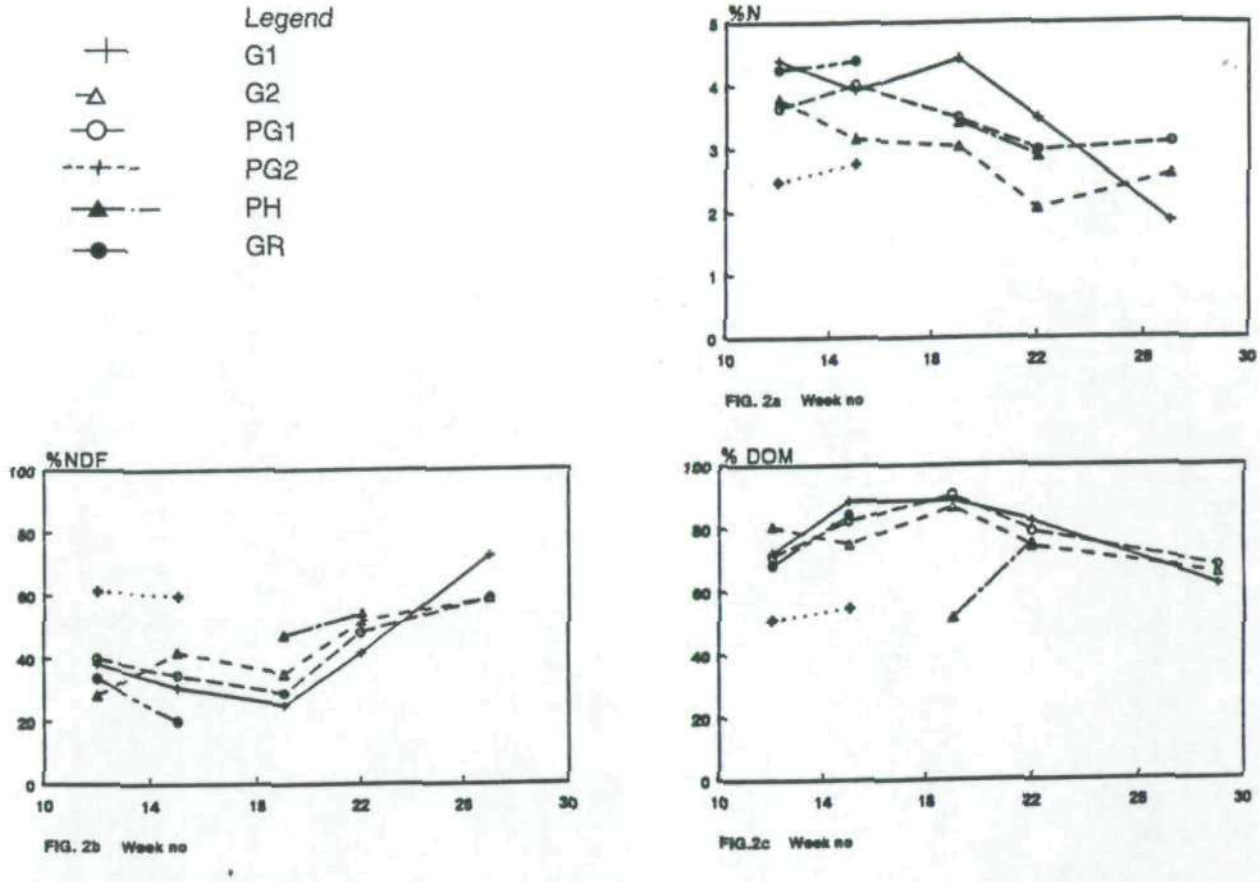


Figure 2. Analysis of bite simulation samples of forage plants (17th March - 2nd July). **2a** crude protein; **2b** cell wall contents; **2c** digestible organic matter.

Figures 1 a,b,c show the results of the analysis of bite simulation samples of forage plants from 17th March up to 2nd July for six of the eight vegetation types. (Appendix IV). Only three of these were sampled on a monthly basis (G1, G2 and PG1), one (PH2) was sampled twice in May/June, and two (PG2 *and GR2) were sampled once during the beginning of the observation period in* April. All samples are mixtures of the different forage plants in the community except the last sample of G1, which consisted solely of flowering Lolium perenne.

The results for April - July are summarized in figure 3, overleaf, by calculating the average for the three analyzed contents over the whole period for the different vegetation types.

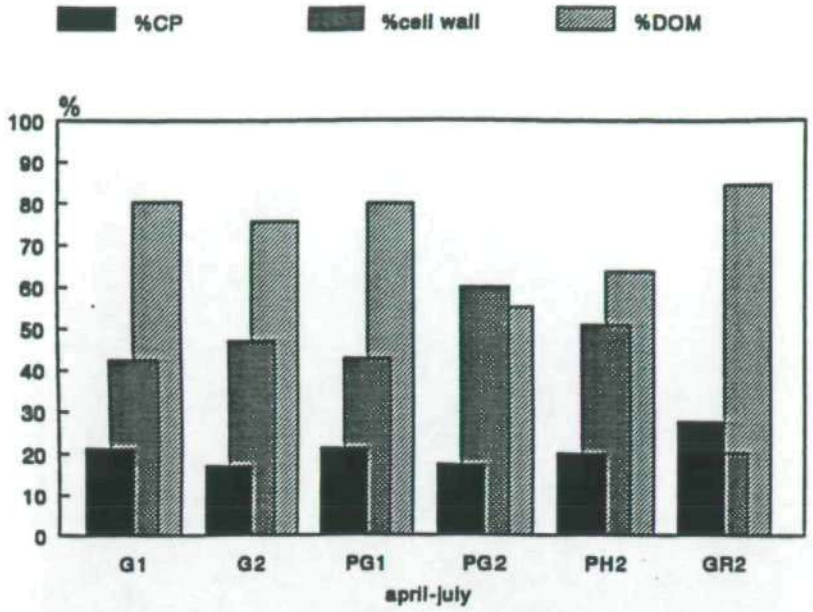


Figure 3. Nutritional values of the vegetation communities.

Both figures clearly show that the analyzed contents of the vegetation types are all above the maintenance level during this period for the daily requirements for Heck cattle (table 1) with the exception of PG2 which has a high percentage of cell wall and the percentage of DOM is below the threshold value of lactating cows. GR2 has extremely low levels of cell wall contents and this is probably caused by the high occurrence of Urtica dioica in the samples. However both PG2 and GR2 cannot be regarded as representative for the whole period (figure 1).

The grassland G1 (and PG1) is of slightly better quality than the grassland G2 (and PG2) because of the high abundance of Trifolium repens (Smit 1992 a & b). PG2 has much denser stands of dead reed than PG1, and the high proportion of reed in the sample is could be responsible for lower values leading to bigger quality differences with PG1 than expected in comparing G1 and G2. For the three vegetation types sampled during the whole period vegetation growth seems to influence the analyzed contents, as can be seen in figure 1 for the downward trend of CP and DOM percentages and rising cell wall percentages. Although it does not really apply in this case, as all the vegetation types are of very high nutritional value, a rank order based on these results has been assigned as follows:

G1	PG1	G2	PH2
Good	→	→	*Less good*

The rank order is based on the contents of cell wall and digestible organic matter in the forage plants as previous research (Vulink & Drost 1991 a, Huijser 1992) and these results show that crude protein is not a limiting factor in the OVP. PG2 and GR2 are not ranked because only one sample of each was made during the observation period. Statistical tests were not applied due to the small sample size.

3.2 Habitat use

3.2.1 Patterns of range use

To determine habitat use by bulls, the home range of the focal animals were delineated by taking in account all the compartments they were observed on for more than 5 minutes. In this way the grazing time on each vegetation type available in the individual's home range could be compared with the expected grazing time on that vegetation (figure 4). The proportion of a vegetation type of a home range to the total area of that home range is used to calculate the expepected grazing time (table 3).

Chi-squared test showed no significant differences between observed and expected grazing time for any of the vegetation types in the individual home ranges. This could mean that the bulls are evenly dispersed over the vegetation communities available to them in their home ranges. However, this is not apparently the case for bull no. 12 for and bull no. 39 (figure 3; they graze more than expected on vegetation types PG2 and PG1) and this implies that chi-squared is not the appropriate test.

Table 3. Time (in min.) spent grazing on the different vegetation types by the focal bulls.

Veg. \ Bull	12	15	24	39	55	59	TOTAL
G1	0	5	377	285	167	0	834
G2	120	109	383	110	264	0	986
PG1	0	353	1	240	0	718	1312
PG2	412	0	18	0	1	0	431
PG3	38	0	0	0	0	0	38
PH2	65	47	9	0	0	111	232
PH	11	0	0	0	0	0	11
GR2	70	0	0	41	227	0	338
path	0	0	0	0	102	0	102
TOTAL	716	514	788	676	760	829	4283

These results show that the home ranges are predominantly on grassland/reed vegetation types. Bull no. 12 shows the most variation in utilizing other vegetation types as these are more available in his home range (Fig. 4a).

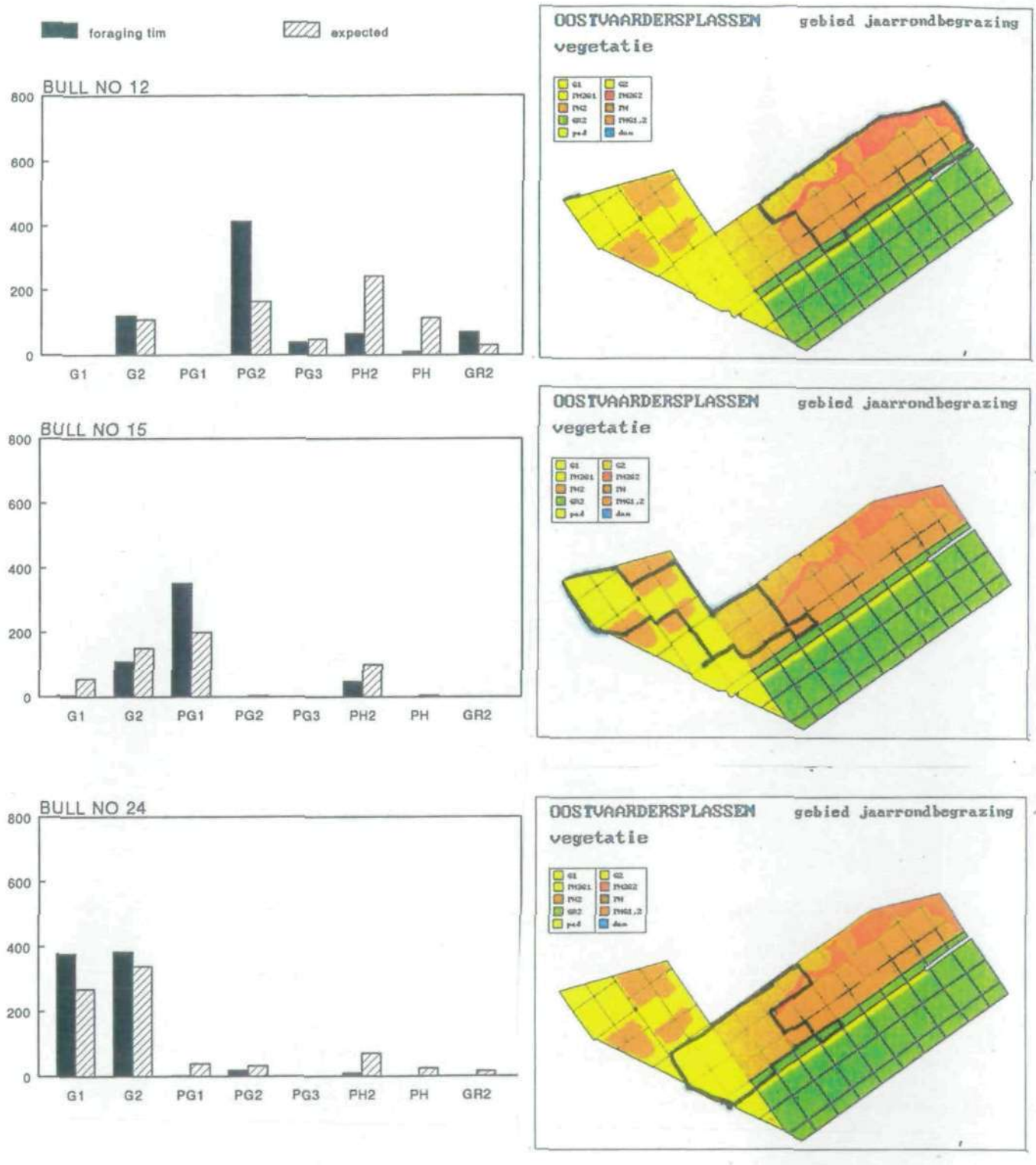


Figure 4 Grazing time and expected grazing time (in minutes) on the different vegetation communities for the six focal bulls in their home ranges (map). (Continued overleaf.)

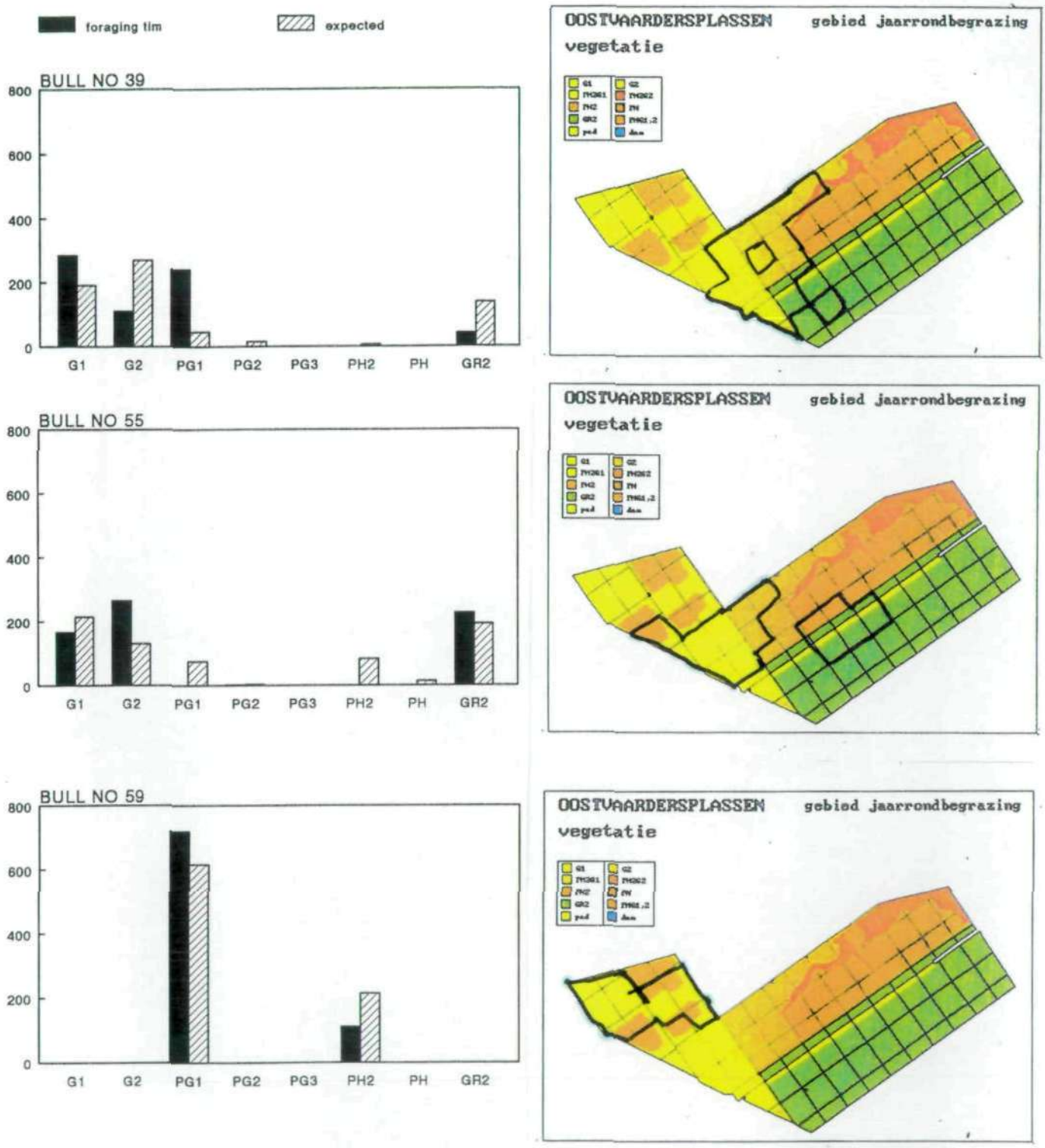


Figure 4 (cont.) Grazing time and expected grazing time (in minutes) on the different vegetation communities for the six focal bulls in their home ranges (map).

Note: Bull no. 55 was observed as a solitary bull for two days, which he spent on GR2 and path vegetation.

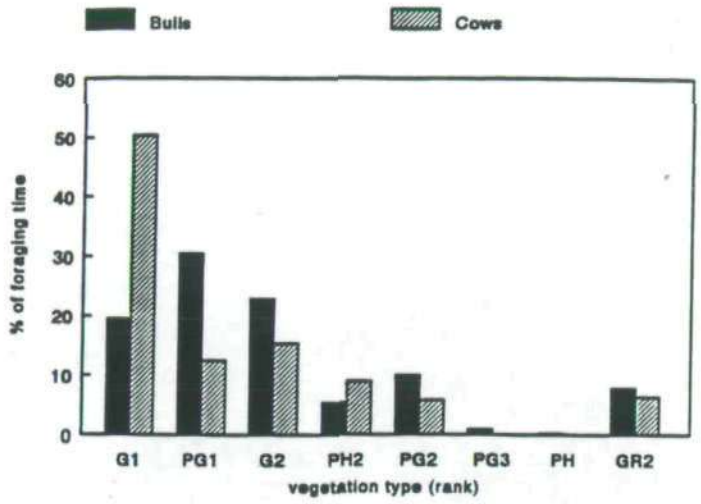


Figure 5 Differences in foraging time between bulls and cows per vegetation type.

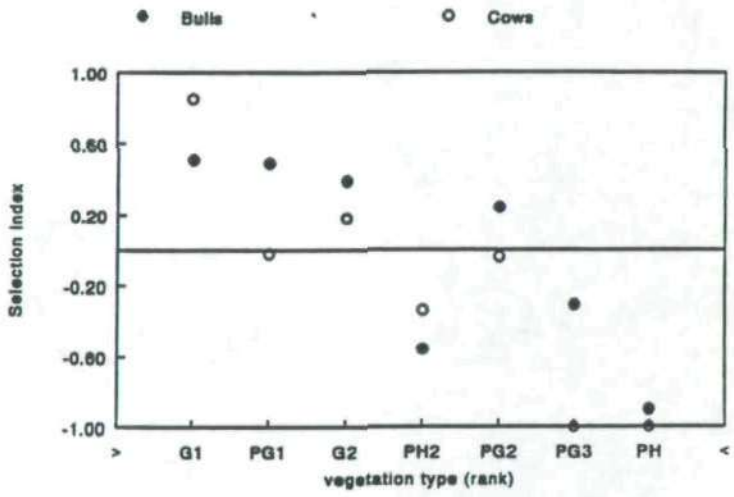


Figure 6 Selection index (E) for bulls and cows per vegetation type.

In comparing foraging time on the different vegetation type between the two sexes it is clear that the two sexes do not have similar patterns of vegetation type use (figures 5 and 6, Appendix IV).

Cows make the highest use of the grassland G1, the only vegetation type for which they make a strong selection. In fact cows only make a positive selection for the two open grassland communities G1 and G2 and are neutral towards the grassland-reed communities. Bulls showed a broader selection for the grassland(-reed) vegetation communities, although selection was stronger for vegetation types including G1 . The reedland vegetation types were avoided by both sexes (Fig 6).

3.2.2 Foraging

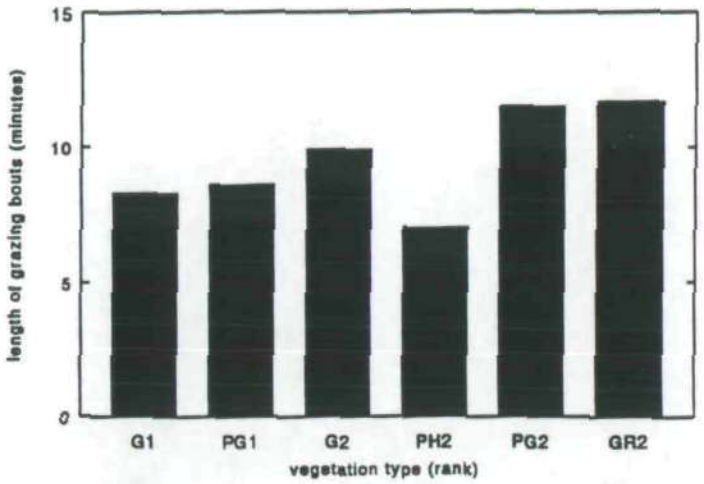


Figure 7 Mean length of grazing bouts.

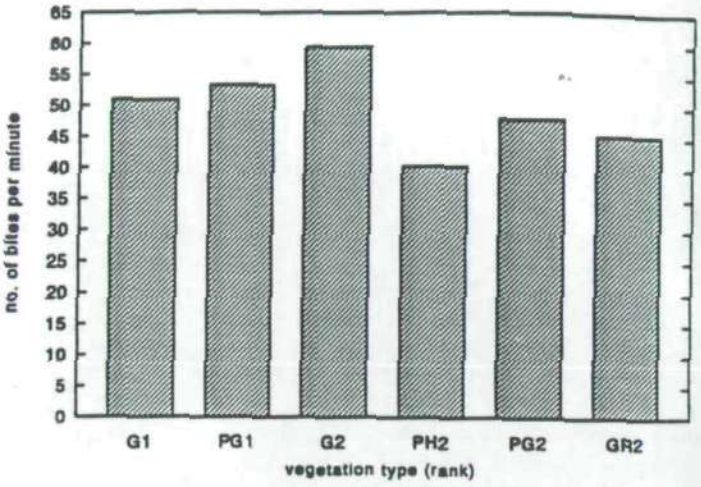


Figure 8 Bite rates per vegetation community.

Besides time spent on foraging, grazing is further delineated as grazing bouts. A grazing bout is defined as the time (in minutes) an animal spends grazing continuously. Mean length of grazing bouts determined for the bulls on the six vegetation types are shown in figure 6. Mean length of grazing bouts varied significantly (Kruskal Walliss one-way analysis of variance (K.W.), $p < 0.05$, $n = 516$). The open grassland communities have an intermediate grazing bout lengths of 8 min. and the more dense vegetation communities (PG2 in terms of reed, GR2 in terms of wood plants, and higher standing crop) have the longest bout length (c. 11.48 min). Dense reed vegetation with some grass undergrowth has the shortest mean length.
The av. length of grazing bouts for bulls is 8.3 min (S.E. 0.4) and for cows 10.99 min (S.E. 1.28) (Mann Whitney U test, not significant (ns).

Bite rates for the different vegetation types, derived from grazing protocols (fig. 7), also showed significant differences between the vegetation tpes (K.W., $p < 0.05$, $n = 132$). Highest bite rates per minute were observed on the open grassland types, intermediate rates on the denser vegetation and lowest bite rates on the dense reedland vegetation. Cows have lower bite rates than bulls (av. 45.13/min, bulls av. 52.78), but this could not be tested because of the small sample size for cows. Analysis of variance shows that apart from individual variation, vegetation type had a significant influence on the mean length of grazing bouts and bite rates. (ANOVA, $p < 0.01$)

4. SOCIAL STRUCTURE

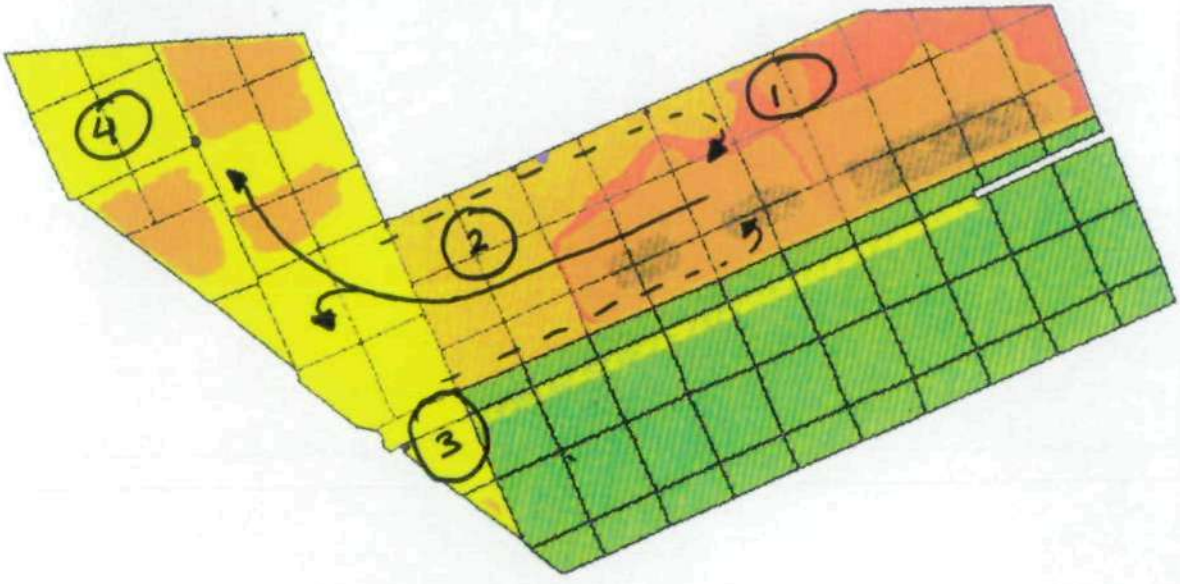
4.1 Bull groups

There are 44 adult bulls in the year-round area and 38 bulls have formed associations resulting in four bull groups. These bull groups are stable throughout the year to a great extent (Blaakmeer *et al.* 1992, Kooi & Rademaker 1992). During the observation period 4 bull groups were distinguished:

	No. bulls	Core area	Focal animal
Bull group 1	9	Compartment D8	12
Bull group 2	10	Compartment C29	24 55
Bull group 3	9	Compartment C30	39
Bull group 4	10	Compartment C27	15 59

Core areas were determined on the basis of scans made from June 1991 until July 1992. There were 3 bulls that seemed to form a loose association on compartment C30 and 3 solitary bulls that roamed the GR2 compartments south of the path ('t stort). More bulls roamed this area in winter but by May had returned to bull group 1 and 2 respectively (Kooi & Rademaker 1992).

The following picture shows the location of the core areas of the bull groups and the range of the main herd for spring/summer.



Legend:
O bullgroup
—> main herd morning and daytime range
---> main herd evening range

In their daily range movements the cows, calves and sub-adults from the main herd frequent the home ranges of all the bull groups. Morning and evening movements usually occur in smaller groups, eventually forming larger groups on the foraging and resting sites.

The bulls in the bull groups all seem to have spent similar amounts of time alone *with bulls in their bull group (av. 40%) and in a mixed herd (av. 60%), when* visited by the main herd (figure 9).

However there is a great amount of variation in the number of individuals from the main herd and the time they spent in the home ranges for the different bull groups (figure 10). The exact numbers and time for the individual bulls are given in Appendix 6. To reflect this for the bull groups (figure 10), the mixed herd they temporarily form when amongst the main herd in their home range has been divided into two categories;

<30	an average of 9/10 bulls and 1 to 19 individuals from the main herd
>30	an average of 9/10 bulls and 20 to 100 individuals from the main herd

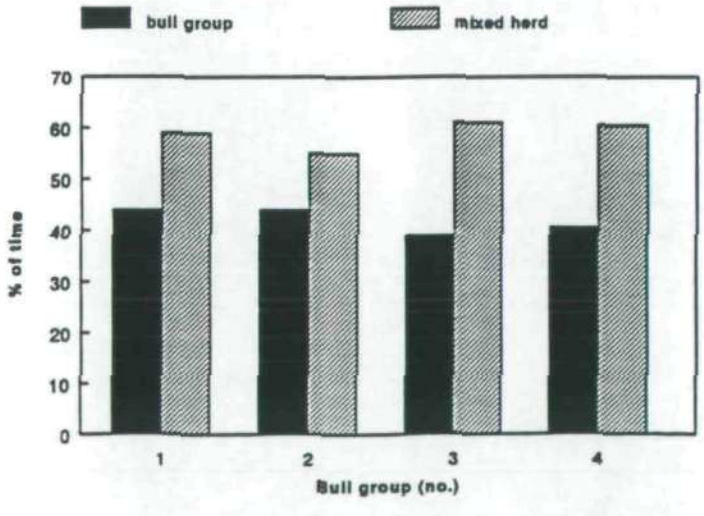


Figure 9 Percentage of time bulls *spent in mixed herd.*

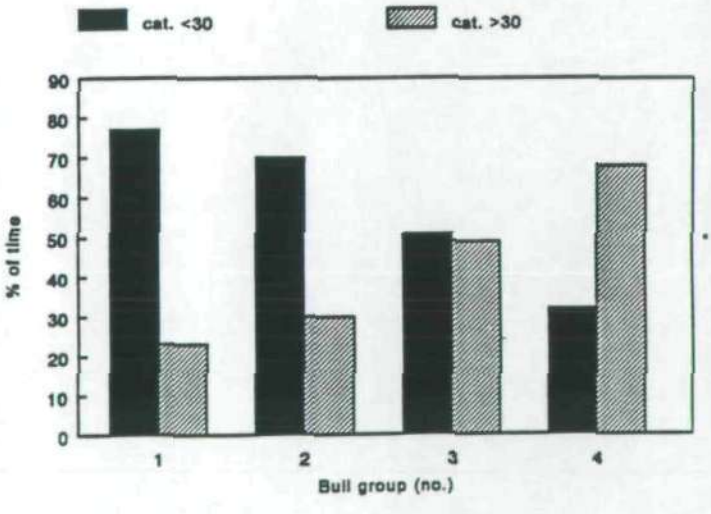


Figure 10 Percentage of time bulls *spent with number of individuals in* mixed herd.

Figure 10 shows that bull groups 1 and 2 spent almost equal times in categories <30 and >30 (c.75% and 25%), bull group 3 spent the same amount of time in both categories and bull group 4 spent more time in category >30 than <30 (68% and 32%). Bull group 4 is visited by a greater number of individuals from the main herd during the day that stay for long periods of time. Bull groups 1 and 2 are frequently visited by small groups of the main herd which remain in their home range for longer periods than large groups, while bull group 3 takes an intermediate position.

4.2 Activity

Time budgets percentages for different activities (Appendix III) by bulls and cows are shown below.

Table 3. Percentage of time spent on activities by bulls and cows

	Stand	Walk	Lie	Graze	Rumin	Interact	Groom
Cows	10.8	12.5	13.9	46.0	12.5	3.5	0.8
Bulls	22.6	7.9	13.8	28.6	13.2	12.9	0.7

Cows spent more time walking and far more time grazing than bulls. Bulls in contrast spent more time standing and engaged in social behaviour.

As the cows' home range covers all the home ranges of the bull groups, cows were always observed in the vicinity of bulls and therefore were always recorded as being in a mixed herd. This is not the case for bulls who were recorded as being in a mixed herd, bull group or as a solitary bull.

To compare the differences in time spent on basic activities when in a bull group or in a mixed herd, the total time spent by each focal bull in the different groups on these activities are given in figure 11 (overleaf).

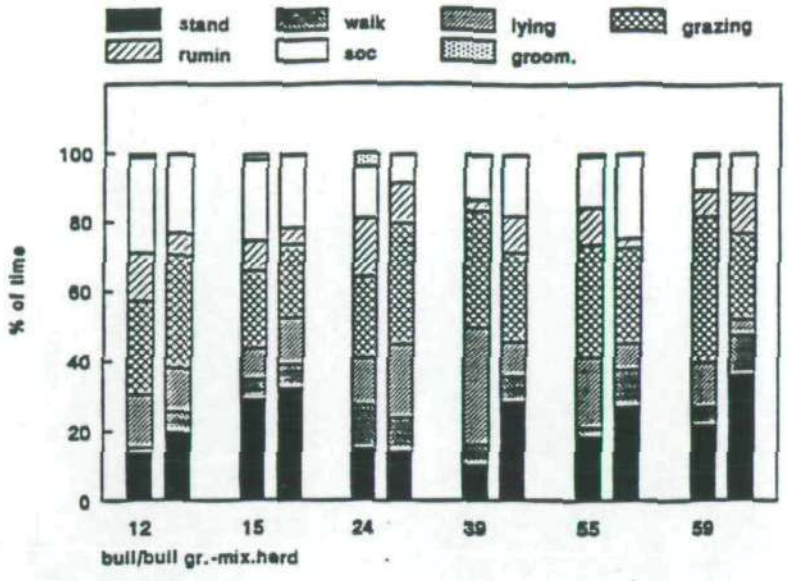


Figure 11 Percentage of time spent on activities by focal bulls while in a bull group or mixed herd.

In the first place, for each focal bull there were no significant differences for the time spent on the different activities whether he was in bull group or in a mixed herd. Bull no. 39 spent much more time lying when in a bull group but Kruskal Wallis one way analysis of variance depicted too many ties so there was no outcome.
In the second place there were no significant differences between the bulls for time budgets spent on the different activities, whether in a bull group or in a mixed herd. The only significant difference found was for walking (K.W. $p<0.05$) which is explained by the large amount of time spent walking by bull no. 24 when he is in a bull group.
The percentage of time spent on the activities in bull groups and mixed herds, for the bulls grouped together, is shown below:

Table 4. Comparison of percentages of time bulls spent on activities in the absence or presence of cows.

	Stand	Walk	Lie	Graze	Rumin	Interact	Groom
Bull group	18.2	5.5	17.3	30.2	10.1	17.3	1.4
Mixed herd	26.1	8.5	11.5	27.8	7.9	17.7	0.2

The overall picture is that bulls stand and walk more when visited by the main herd at the 'expense' of lying and they ruminate and groom more when among bulls only. There is no difference in the time they spent grazing or engaged in social behaviour (i.e. interactions involving the focal animal and at least one other animal).

However if a distinction is made between time spent on social behaviour between bulls, when they are in a bull groups or in a mixed herd, bulls spent a greater amount of time on interactions among each other in absence of the mixed herd (6.4%) then when among cows (3.4%).

Grazing was further delineated as grazing bouts, i.e. the time the focal animal spends grazing continuously, and there is a significant difference in the mean length of bout durations between the two social groups, and within the mixed herd between the two categories.

The mean length of grazing bouts in bull groups is 10.45 minutes ($n = 169$) and in mixed herds 7.1 minutes. In the mixed herd category <30 the mean length was 8.5 minutes ($n = 173$) and in category >30 it was 5.6 minutes ($n = 174$) (K.W. $p < 0.01$ $n = 516$). Grazing bout duration also showed correlation with the number of animals as defined in the categories (Spearman rank correlation = -0.17, $p < 0.01$).

5 DISCUSSION

5.1 Habitat use

Differences in body size lead to differences in energy, nutrient and digestibility requirements. Basal metabolic rate decreases non-linearly with body weight. This means that, although large animals always require more total energy, small animals require more energy relative to their body weight.
Retention time determines intake and digestion rates and depends on rumen volume and gut capacity, which increase linearly with body size. Therefore large herbivores can extract more energy and nutrients from plant material, because longer retention times produces higher digestibility of forage components. Retention times will be shorter for smaller animals which implicates they will select food composed of a more rapidly digestible fraction. (Demment & Van Soest 1984).

The average weight of Heck cattle bulls is almost twice as much as that of cows. As breeding takes place all year-round and the observed individual cows had young calves, maintenance requirements for lactating cows seemed a more appropriate measure for comparison (table 1).
Energy demands rise approximately two-thirds, and dry matter intake one-third as opposed to non-lactating cows. Also, requirements for crude protein and digestible organic matter are much higher than those for bulls.
Together with lower bite rates (section 3.2.2) the above explains why cows spend more time grazing than bulls. Even though the quality parameters of the forage samples should have been weighted by the number of observed bites per plant species for the different vegetation types, the nutritional values of all vegetation types, based on the forage samples as analysed here, are above maintenance requirements for the animals during the observation period.
Nevertheless bulls and cows are not evenly distributed over the different vegetation types. Cows spent most of their foraging time on vegetation type G1, which overall is the sward of the highest quality and this strong selection supports the hypothesis that the daily range movement of the main herd is based on a diet selection to optimize nutrient (especially protein and digestible organic matter) intake.
Bulls, having lower quality demands, could afford to confine themselves to parts of the area where quantity measures are met, thus reducing competition for resources with cows. This seems highly unlikely for the time of the year when quality and standing crop are high, but this could apply for the winter period. Although restricting their daily range, cows retain a strong selection for G1 throughout the winter period (Kooi & Rademaker 1992). Nutritional values do not fall below threshold values but during the first months of the year standing crop is reduced to an average minimum level of c. 2.5 cm on the open grasslands (Huijser 1992). (For these data analyses, two vegetation communities were distinguished for the area excluding the GR2 compartments. Therefore it is not possible to make a comparison for the eight communities on the different compartments as described in 'study area').

By incorporating bite size and metabolic requirements relative to body size in a simulation model, Illius and Gordon (1987) show that smaller animals are able to subsist on shorter swards than large animals. They predict that among dimorphic species weight differences of more than 20% could lead to ecological separation. Therefore it could be possible that continuing high grazing pressure by the main herd on the G1 compartment in winter reduces the standing crop on this compartment to such a level that the larger bulls turn to compartments with higher standing crop.
This has also been found in the case of red deer on Rhum, where lowered biomass in winter and increasing population density resulted in a competitive exclusion of stags by hinds on the mutually preferred short grasslands (Clutton-Brock *et al.* 1987). During the winter period some of the bulls of bull group no.2 (vegetation types G1 & G2) left their home range for the GR2 compartments (Kooi & Rademaker 1992) which sustain higher biomass of grasses and forbs among the dead reed. The bulls of bull groups 1, 3 and 4 have located their home ranges in parts of the area which include large parts where standing crop is significantly higher and forage quality is lower than on the open grasslands (Huijser 1992). Furthermore the home ranges of bull groups 1 and 3 are in the vicinity of the compartments with vegetation type GR2 ('t stort) and the main herd does not visit the home range of bull group 4 in winter time (vegetation types PG1 and PH).

The dissimilar patterns of habitat use between the sexes has resulted in a situation where parts of the area are subjected to a continuous grazing pressure by bulls. Herewith the main question of the research project (introduction) is re-addressed. Considering the number of bulls per bull group and daily dry matter intake (table 1) this leads to an average daily consumption of c. 150 kg of dry matter per day in each of the four observed home ranges with a variety of vegetation types. The vegetation of the area has also been classified according to reed height and monitored since 1987 (Huijser 1992). Comparison between the years 1990 and 1991 shows a considerable reduction of intermediate and high reed classes notably on the C27 and upper C30, D8, and D9 compartments (Appendix I and II). These compartments coincide with the home ranges of bull groups 4 and 1 respectively (fig. 7).
The foraging activities of the main herd is largely concentrated on the G1 and G2 compartments throughout the year and extends to the PG1 compartments during spring and summer. The former two are important grazing areas for geese (Huijser 1992). Huijser concludes that grazing by the herds of Heck cattle and Konik horses are responsible for creating and maintaining open grassy vegetation communities, supporting management objectives. The results of these studies show that the influence of the social structure of the herd of Heck cattle upon the area makes a substantial contribution, due to the formation of bull groups.
As mentioned before competition for resources does not explain why bulls confine themselves to smaller parts of the area during the whole year. One reason could be that this is a consequence of the winter situation and it is continued because of habituation or territorial behaviour.

However another factor that could influence condition and hence reproductive success is competition for females. If all the adult bulls were to remain in the main herd there would be 44 potential competitors for access to oestrus females. As breeding takes place all year round agonistic behaviour among bulls could lead to high energetic costs, reduced foraging time as well as higher risks of injury (Gosling 1986). Food abundance and quality are high for most part of the year and the formation smaller groups could decrease the amount of disturbance.

However if reproductive success is the reason, a condition to form bull groups in parts of the area is that these areas are visited by females. From spring to autumn all the home ranges are arranged in such a manner that they are in a part of the range of the daily movements of the main herd (section 4.1). This means that all the bull groups are visited by cows during some part of the day and fig. 9 shows that all the bull groups spent equal amounts of time in a mixed herd during daylight. This could imply that the bulls have chosen to detach themselves from the main herd to retain adequate foraging time and so are able to spend their time on social behaviour when the cows visit. However time budgets spent on different activities for bulls when in absence or presence of cows only showed that bulls walk and stand more in a mixed herd (fig. 10) and lie less. These activities cannot be regarded as having a high influence on energy costs.

Time spent grazing is the same for the two social groups, but the difference in the mean length of grazing bouts (fig. 11) indicates that the presence of more individuals from the main herd is a distracting factor. Length of grazing bouts did not correlate with the number of bulls when grazing in a bull group ($r_s = -0.0213$, $p = 0.78$, $n = 169$), and therefore the distraction can be attributed to the presence of cows. When bulls are in the vicinity of cows olfactory encounters involving sniffing and flehmen are frequently observed. Inspecting cows for clues of reproductive status increases when more cows are present (pers. obs.) and although it does not reduce foraging time, grazing bouts decline probably as a consequence of this (voluntary) behaviour. This is supported by the fact that the time spent on interactions among bulls (most of which can be described as agonistic behaviour) decreases when they are in the presence of cows (see page 23). Overall, bulls spent almost twice as much time engaged in interactions amongst each other in bull groups .

This could mean that hierarchy among bulls is determined in the absence of cows. Assuming social ranks are established during interactions in bull groups, the most dominant bull from the bull group will have access to prime females when the main herd visits the home range. This decreases the amount of disturbance when they are in the mixed herd as all the bulls know their rank and presumably will act in accordance of it. This could be an important factor for the formation of bull groups because reducing the number of competitors, by detaching from the main herd, enhances the individual's chance for reproductive success.

Retaining dominance over nine or ten competitors in the absence of cows can be assumed to be more successful than over forty-four competitors in the presence of cows. Furthermore reducing the number of competitors is also beneficial for lower ranking bulls as there is a greater chance of acquiring a

(more) dominant status when the most dominant or higher ranking bulls should 'fall in rank' because of old age, injuries or displacement by an other bull.

Even though all the bulls spent similar amounts of time in the mixed herd figure 8 shows that there is a difference in the number of individuals from the main herd that visit the bull groups and the amount of time they spent in the home ranges. These results indicate that the home range of bull group no. 4 has the best location regarded in terms of mating strategy, because it is visited more often by a larger number of potential mates in spring and summer. Even though breeding takes place all year-round there is a birth peak in spring (Blaakmeer *et al.* 1992). The gestation period for Heck cattle is nine months (A. Hoekstra pers. comm.) and this implies that most of the copulations will occur in summer.

When a cow is in oestrus she is 'guarded' by a bull who will attempt to keep other bulls at bay and mate with her (Blaakmeer *et al.* 1992). However, cows roam freely throughout the area and are not deterred by the territorial and guarding behaviour of the bulls. This means that a bull must try to achieve mating during the time receptive cow is in the bull group's home range. Attempts to mate were observed regularly but only once a successful mating was recorded.

This event took place at dusk on compartment D8 the home range of bull group no. 1, between bull 12 and a receptive cow. This is part of the range where the main herd gathers to shelter at night in the PH vegetation, although in summer they were also recorded resting on C29 for the night. Two successful matings were recorded around dusk during field observations days in summer 1991 and winter 1992 (Blaakmeer *et al.* 1992, Kooi & Rademaker 1992) and therefore one could assume that most copulations take place between dusk and dawn.

Therefore, though it seems that the home range of bull group 4 has the best location during daylight in regard to cow visits, bull groups 1 and 2 probably have their home ranges better located in terms of mating strategy, because these are in the area where the main herd spends the night. Also the main herd does not move up to the C27 compartments (bull group 4) in the winter period. Surprisingly most of the bulls from bull group 2 were introduced in 1989 (Blaakmeer *et al.* 1992) whereby these bulls have acquired the home range which includes the most selected vegetation type by cows and where cows spend the night during the summer period.

From these results it seems that the formation of bull groups is foremost a mating strategy. This seems to have a positive effect for the main herd in terms of competition for resources on the most selected sward and a reduction in agonistic behaviour (disturbance levels) amongst bulls when the main herd is present. The territorial behaviour of the bull groups indicate that despite high forage quality and quantity for most part of the year, and the even amounts of visits of the main herd during daylight, the location of the home range is of main importance.

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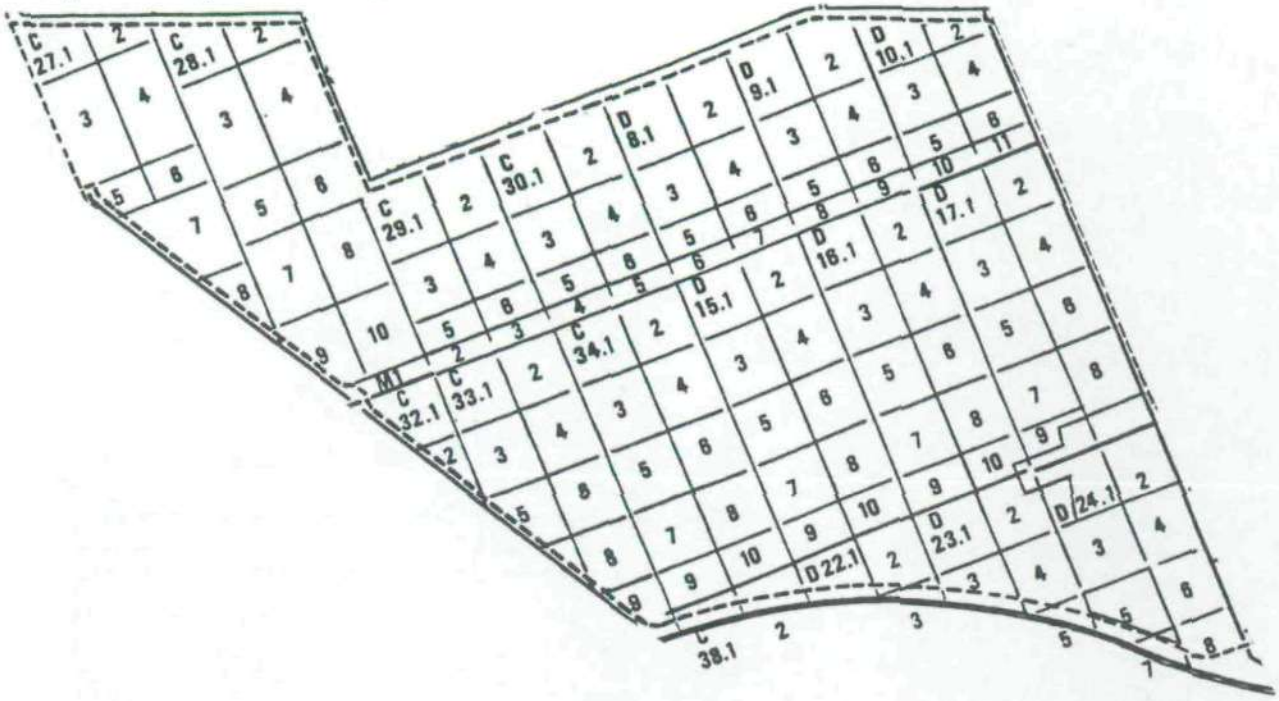
APPENDIX I

Map of the year-round grazing area, including compartment codes



APPENDIX II

Vegetation map of the main part of the year-round grazing area